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PAPERS OF THE MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

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VOLUME XXVIII (1942)
PART II: ZOOLOGY

"Pusilla res mundus est nisi in illo
quod quaerat omnis mundus habeat."
— SENECA, *Naturales Quaestiones*

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CONTENTS

PAGE

Annulus Formation on the Scales of Certain Michigan Game Fishes. William C. Beckman 281

A Test of Fecundity of the Garter Snake *Thamnophis sirtalis sirtalis* (Linnaeus) in the Year Following the Year of Insemination. Frieda Cobb Blanchard 313

Female Allotype of *Landana spinosa* Petrunkevitch. Arthur M. Chickering 317

The Genus *Vespula* (Hymenoptera, Vespidae) in Michigan, with Keys and Distribution. Robert R. Dreisbach 323

Mathematical Relationship between the Length and the Age of the Rock Bass, *Ambloplites rupestris* (Rafinesque). Ralph Hile 331

Mass Hybridization between Two Genera of Cyprinid Fishes in the Mohave Desert, California. Carl L. Hubbs and Robert R. Miller 343

The Mosquitoes of Three Selected Areas in Cheboygan County, Michigan. William H. Irwin 379

The Breeding Habits of the River Chub, *Nocomis micropogon* (Cope). Jacob Reighard 397

Origin of Diverse Strains of an Aphid Species within a Limited Area. A. Franklin Shull 425

ILLUSTRATIONS

PLATES

BECKMAN: FACING PAGE

Pl. I. Ctenoid scale from a bluegill; cycloid scale from a cisco . 312

Pls. II–IV. Scales of bluegills 312

DREISBACH: Pls. I–IV. Male genitalia of species of *Vespula* in Michigan 330

HUBBS AND MILLER:

Pl. I, Figs. 1–3. Scales of *Gila orcuttii*, *Siphateles mohavensis*, and hybrids 378

Pl. I, Fig. 4. Lowest pool of Deep Creek, in the Mohave Desert, California 378

Pl. II. Specimens of *Gila orcuttii*, *Siphateles mohavensis*, and hybrids 378

Pl. III. Pharyngeal arches and teeth of *Gila orcuttii*, *Siphateles mohavensis*, and hybrids 378

Pl. IV. Gill arches of adult minnows of *Gila orcuttii*, *Siphateles mohavensis*, and hybrids 378

FIGURES IN THE TEXT

BECKMAN: PAGE

Fig. 1. Map showing location of Michigan lakes from which scales of game fishes were collected 283

Fig. 2. Chart showing percentage of "expected" annual scale growth completed on different dates in 1939 by yearling bluegills from Pasinski Pond 300

CHICKERING: Fig. 1. External anatomy of *Landana spinosa* Petrunkevitch 318

HUBBS AND MILLER:

Fig. 1. The present drainage features of the Mohave River system and vicinity, Mohave Desert, California 344

Fig. 2. Detail of the headwater portion of the Mohave River system 344

REIGHARD: Fig. 1. Diagram showing the usual locus of fishes breeding on a stone-pile nest of the river chub, *Nocomis micropogon* 421

ZOOLOGY

ANNULUS FORMATION ON THE SCALES OF CERTAIN MICHIGAN GAME FISHES *

WILLIAM C. BECKMAN

THIS investigation on the annulus formation on the scales of Michigan game fishes was begun in September, 1938, when the writer undertook the growth-rate studies for the Institute for Fisheries Research of the Michigan Department of Conservation. It soon became apparent that one of the first problems was to delimit the time or period of year at which the annulus or year mark forms on the scales of certain of the game fishes of Michigan. The precise determination of the age of fish collected in spring and early summer was difficult, and at times impossible, because of the lack of exact information on the time of annulus formation. On many scales it was hard to decide whether the marginal area outside the last annulus represented the new season's increment or the entire last year's growth. If the year mark of the previous winter had already formed, the age as determined by the number of completed annuli would be correct, but if the mark had not been completed, the fish would be one year older than the age indicated by the number of annuli.

In order to solve this main problem conclusively it was necessary to demonstrate that the annulus on the scale of the fishes studied corresponds structurally with the year marks which have been found in various species by other workers, and to secure evidence that the annulus is formed each year and only once annually.

It was apparent, also, that the solution of the problem of the time of annulus formation would contribute in other ways to an understanding of fish growth. For instance, evidence would be secured on the factors responsible for the formation of the annular rings. The periodic sampling would make it possible to determine at which part of the growing season the growth is fastest. It would be possible, also, to trace the course of growth during one season. Furthermore,

* Contribution from the Institute for Fisheries Research of the Michigan Department of Conservation.

an analysis could be made of possible differences in the growth of the sexes, and of various age groups and sizes of fish. Although data were obtained on all these problems, this report is concerned primarily with the time and cause of annulus formation.

The writer is indebted to the Michigan Department of Conservation, whose Institute for Fisheries Research furnished all equipment and expenses for the study as well as financial aid in the form of an assistantship on its staff. Acknowledgment is made of the assistance and direction given during the investigation by Dr. A. S. Hazzard, director of the Institute. The writer also wishes to thank the various members of the Institute staff, other employees of the Fish Division of the Michigan Department of Conservation, and all others who helped further the investigation. For guidance and valuable advice throughout the course of graduate study and in carrying out this investigation he wishes to thank Dr. Carl L. Hubbs, of the University of Michigan. Thanks are also due to Dr. Ralph Hile, of the United States Fish and Wildlife Service, for his assistance and advice.

SOURCE OF MATERIALS

For the monthly collection of scale samples which comprise the material used in this investigation eight waters (seven lakes and a pond; Fig. 1) were selected at the beginning of the work. These waters were chosen so as to insure a range of samples for several species from south to north. Collections were made of the species listed at the following places on the dates given:

Clear Lake, Jackson County (area, 137 acres; maximum depth, 35 feet):[1] January, February, April, June, July, and December, 1939, and May and June, 1940. Game species: yellow perch (*Perca flavescens*), largemouth bass (*Huro salmoides*), bluegill (*Lepomis m. macrochirus*), pumpkinseed (*Lepomis gibbosus*), rock bass (*Ambloplites r. rupestris*), and black crappie (*Pomoxis nigro-maculatus*).

Pasinski Pond, Livingston County (area, 4½ acres; maximum depth, 5 feet): September, 1938, April, May, June, July, and September, 1939, and February, 1940. Game species: bluegill.

Budd Lake, Clare County (area, 175 acres; maximum depth, 34 feet): May, June, and October, 1939, and May and June, 1940. Game species: yellow perch, largemouth bass, bluegill, pumpkinseed, rock bass, and black crappie.

Round Lake, Emmet County (area, 336 acres; maximum depth, 27 feet): May, June, and October, 1939, and May and June, 1940. Game species: perch, largemouth bass, bluegill, pumpkinseed, and rock bass.

[1] The descriptive statements regarding each lake are taken from the maps and survey records of the Institute for Fisheries Research.

FIG. 1. Location of the lakes from which the major collections were made and limits of the three temperature zones into which the state was divided

North Manistique Lake, Luce County (area, 1,722 acres; maximum depth, 50 feet): June, July, September, and October, 1939, and May, June, and July, 1940. Game species: yellow perch, walleye (*Stizostedion v. vitreum*), smallmouth bass (*Micropterus d. dolomieu*), and rock bass.

Bass Lake, Marquette County (area, 400 acres; maximum depth, 30 feet): June, July, September, and October, 1939, and May, June, and July, 1940.

Game species: yellow perch, walleye, smallmouth and largemouth bass, bluegill, and pumpkinseed.

Crooked Lake, Gogebic County (area, 566 acres; maximum depth, 66 feet): July, August, September, and October, 1939, and May, June, and July, 1940. Game species: yellow perch, smallmouth and largemouth bass, bluegill, pumpkinseed, and black crappie.

Lake Fannie Hooe, Keweenaw County (area, 231 acres; maximum depth, 48 feet): July, August, September, and October, 1939, and May, June, and July, 1940. Game species: yellow perch, smallmouth bass, bluegill, and rock bass.

In connection with other investigations for the Institute for Fisheries Research some data were taken on three additional lakes:

Standard Lake, Cheboygan, Charlevoix, and Otsego counties (area, 32 acres; maximum depth, 31 feet): May, June, and October, 1939, and May, 1940. Game species: yellow perch, smallmouth bass, and rock bass.

Ford Lake, Otsego County (area, 12 acres; maximum depth, 39 feet): May, 1939, and May, 1940. Game species: bluegill.

Deep Lake, Oakland County (area, 15 acres; maximum depth, 61 feet): February, April, May, June, July, and August, 1939, April, May, June, July, August, and September, 1940, and April, May, June, July, August, and September, 1941. Game species: largemouth bass, bluegill, pumpkinseed, and rock bass.

COLLECTION, PREPARATION, AND EXAMINATION OF SCALE MATERIAL

The collections were made with three to nine gill nets (5 by 125 feet, of five mesh sizes, grading from $1\frac{1}{2}$ to 4 inches, stretched measure), with seines, and with a river fyke net (9 feet long, with 5-foot wings and made with 2-inch stretched-measure mesh). Rod-and-line fishing also was employed in the taking of samples.

Length, weight, sex, and state of sexual maturity were recorded, and scale samples were taken. Both standard length, the length of the fish from the tip of the snout to the end of the vertebral column, and total length, the greatest measurable length of the fish, were recorded to the nearest millimeter. All weights were recorded to the nearest gram, with the exception of those of a few large fish (walleyes), which were weighed to the nearest half ounce.

In the laboratory the scales were prepared in the customary manner and mounted on glass slides in a glycerin-jelly medium. They were examined on a projection machine similar to the one described by Van Oosten, Deason, and Jobes (1934). Measurements were made along the most nearly vertical anterior interradial space. The positions of the annuli were marked on 1- by 11-inch tagboard strips.

Measurements in millimeters for computations were taken from these strips.

The data were tabulated on "growth-analysis cards" used by the Institute for Fisheries Research, according to species, date of collection, sex and age group, and under age group by size.

THE SCALE METHOD

This investigation is designed to render more precise the determination of the age of fishes by the scale method. The age of the fish is determined by counting the number of annuli or year marks on the scale. The general validity of this method has been assumed. That the annuli on the scales do provide a clue to the fish's age and growth has been demonstrated for many species and is now confirmed for the material used in the present study.

The structure of the scale and the character of the annulus are described below. All the fishes used in the present study have ctenoid scales, which may be exemplified by a photograph (Pl. I, Fig. 1) of a scale from a bluegill, $4\frac{1}{4}$ inches long, caught on June 14, 1939, in Pasinski Pond, Livingston County. In the center of the scale is a very small clear area, the focus, which represents the original scale of the young fish. Around this center are numerous ridges or circuli, which represent successive stages in scale growth, though they seldom correspond exactly with the scale margin. The posterior or free part of the scale bears the ctenii. On the anterior, concealed, field are the radiating grooves, known as radii.

As the scale grows, each circulus is laid down first along the anterior margin and gradually grows around the scale. A close examination usually will show several incomplete circuli along the dorsal and ventral borders of the scale (left and right in the figure). During the winter, growth is retarded or ceases entirely, and the circuli do not grow to completion. With the resumption of rapid growth in the spring a new circulus is laid down which soon grows around the entire scale margin, just outside the incomplete circuli of the previous growing season, which remain as they were in the winter. The new circulus therefore cuts across these incomplete circuli, and this "cutting over" is one of the most conspicuous and trustworthy characteristics of the annulus or year mark.

The cycloid type of scale lacks ctenii. The circuli usually extend around the entire scale, although they may be weak or absent on the

posterior portion. The annulus is formed in the same general manner as on the ctenoid scales, and is recognized by the same criteria. On examination of the scale (Pl. I, Fig. 2) from an 11-inch cisco (*Leucichthys artedi*), caught on December 1, 1934, in Blind Lake, Washtenaw County, it will be seen that there is an alternation of light and dark bands, made up respectively of widely and narrowly spaced circuli. These bands are usually more pronounced on the cycloid scales, although some ctenoid scales exhibit them also, and some scales of either type do not show them.

Early workers treated these distinct zones as summer and winter bands, but failed to define the incomplete circuli as the chief diagnostic character of the annulus. Hoffbauer (1898, 1900), however, had described the true character of the annulus, and had offered proof of its validity as a year mark. Other works of his (1901, 1904, 1905, 1906) provided confirmatory evidence. Masterman (1913) also pointed out the true nature of the annulus on the salmon scale, as Hoffbauer had done for the carp. Nevertheless, many workers (Gilbert, 1922; Snyder, 1923; and others) continued to interpret the "winter band" as the year mark.

The annuli formed on the scales of the game fishes of Michigan that were studied are of the same character as those described by the majority of workers.

Reviews of the literature and bibliographies on the scale method have been given by Thomson (1904), Taylor (1916), Hutton (1921), Creaser (1926), Mohr (1927, 1930, 1934), Graham (1929), and Van Oosten (1929).

The assumption that the annulus is a year mark and that but one annulus forms each year has been and still is under criticism. This question has been studied in a number of experiments. Hoffbauer (1898 to 1906), in presenting the major foundation of the method, followed the growth of carp of known age in a pond for three years, and made observations concerning the scale characteristics of several other species (*Carassius carassius, Lucioperca sandra, Abramis brama, Esox lucius, Leuciscus erythrophthalmus, and Leuciscus cephalus*). By laboratory or pond experiments Dahl (1911), Mohr (1916), Van Oosten (1923), Creaser (1926), and others furnished basic information on annulus formation. Johnston (1905, 1907) and many later workers, for example, Hutton (1909, 1910), Gilbert (1913), and Fraser (1921), tested the theory by tagging experiments.

Lea (1910), Hjort (1914), and others, in following the dominant year class through commercial catches for several years, determined that one additional annulus appeared on the scales of members of this year class each year. Lea (1911), Fraser (1916, 1917), and others traced the marginal scale growth throughout the year by periodic sampling, and thus obtained evidence to show that only one annulus a year was formed by the species studied.

Contrary evidence also has been gathered which tends to indicate that the determination of the true annuli may not always be a simple matter. Other marks have been described on scales, which, though not true annuli, are often mistaken for them. Jacot (1920) believed that the annulus of the mullet was a migration check. Spawning marks have been described on many scales (Johnston, 1905; Calderwood, 1911, 1914; Hubbs and Cooper, 1935). Hubbs (1921) also described a "metamorphic annulus" on the scales of viviparous perches (Embiotocidae), brought about by a temporary retardation of growth at birth, in the summer. Bennett, Thompson, and Parr (1940) observed that several annuli may form in one season on the scales of a certain percentage of bluegills and largemouth bass in Illinois. Further discussion of this subject will be made in later sections.

FACTORS OF ANNULUS FORMATION

The formation of the annulus is obviously dependent upon the retardation or cessation of growth, followed by a resumption of growth. As Van Oosten (1923) pointed out, growth of the body and scale is closely correlated, and any factor affecting the growth rate of the body may be of primary significance in the formation of the annulus. The problem, then, is largely one of determining the factors that are responsible for the seasonal growth rhythm of the fish.

Temperature

Many authors have held that temperature is the most important factor in the formation of the annulus. The views of Fulton (1904) are as follows: "Temperature is active in modifying the rate of growth by acting directly upon the metabolism of the fish and also by affecting the rapidity of digestion. In very cold water the fishes give up feeding altogether, because the ferments upon which digestion depends do not act, or act very slowly, at low temperatures, and

in fishes, as in other animals, appetite waits on digestion, and this is, on the other hand, correlated with the metabolism in the tissues. It has been shown by Krukenberg that the pepsine or analogous body in the stomach of fish acts as well at 20° C. as at 40° C., at which, among mammals, digestion is most active, and that the rapidity of its action is closely related to the temperature, and Knauthe and Zuntz have shown that the same thing applies to the metabolism in fish, the vital activities being more active in the higher temperature, as shown by the excretion of carbonic acid gas and other products of metabolism."

Thomson (1904) held that "the divergence in growth of the scales during summer and winter is probably due to changes in the general metabolism of the body, which are in their turn, in all probability, the result of seasonal variation in temperature and food supply."

In 1911 Lea stated that there was no close dependence between temperature and growth rate, but that the rate of growth rises as soon as the temperature begins to rise in the spring.

Cutler (1918) wrote in regard to temperature: "The conclusions which I draw from the results of these experiments on the scale growth of fish is, that the broad summer bands, which are caused by the sclerites during the period being wide, and the narrow winter bands, produced by narrow sclerites, are due to changes in the temperature of the water in which the animals live. High temperatures, such as are found in summer months, lead to formation of broad sclerites, while narrow ones are called forth by low winter temperatures."

Van Oosten (1923) stated that "temperature appears to be a primary factor in the formation of annuli in the adults, but only a secondary one in the immature fish."

To determine at just what temperature the annulus forms in southern Michigan a thermograph was set up at Deep Lake, Oakland County, on April 22, 1940. It was removed in September and reinstalled on April 18, 1941. The temperature records for the period during which the annulus formed are summarized in Table I.

The data obtained by means of the thermograph indicate that annuli are formed in the spring at a fairly definite temperature. In both 1940 and 1941 no annuli were observed before the mean daily water temperature exceeded 50° F. The mean temperatures of the days on which the collections first showed annulus formation were 53° F. (May 10) in 1940 and 52° F. (April 22) in 1941. The mean

TABLE I

TEMPERATURE RECORD FOR DEEP LAKE DURING PERIOD OF ANNULUS FORMATION

The thermocouple was located on a shaded area of sandy shoal, on bottom at depth of 18 inches. The dates of annulus formation were May 8–20 in 1940 and April 22–May 5 in 1941.

Week	Temperature, degrees Fahrenheit (Centigrade in parentheses)		
	Mean minimum	Mean	Mean maximum
April 28–May 4, 1940	42 (5.6)	45 (7.2)	49 (9.4)
May 5–11, 1940	49 (9.4)	52 (11.1)	56 (13.3)
May 12–18, 1940	52 (11.1)	55 (12.8)	59 (15.0)
May 19–25, 1940	53 (11.7)	57 (13.9)	60 (15.6)
April 21–27, 1941	48 (8.9)	51 (10.5)	54 (12.2)
April 28–May 4, 1941	56 (13.3)	60 (15.6)	64 (17.8)
May 5–11, 1941	55 (12.8)	59 (15.0)	62 (16.7)
May 12–18, 1941	55 (12.8)	59 (15.0)	62 (16.7)

temperatures of the first days on which a majority of the fish in the collections had formed annuli were 58° F. in both 1940 (May 13) and 1941 (April 28). It should be noticed particularly that the annuli were completed approximately two weeks earlier in 1941 than in 1940, but that the temperatures at the time of annulus formation were almost exactly the same in the two years.

Markus (1932) determined that largemouth bass did not feed readily at 10° C. (50° F.) and that at 4° C. (39° F.) none took food voluntarily. From his experiments Hathaway (1927) reached the following conclusions in regard to bluegill, pumpkinseed, and largemouth bass: "When fishes were tested at 20° [68° F.] and then transferred to 10° the food consumption the first week at 10° was, on the average, about one-third of what it had been at the higher temperature. . . . During the second, third, and fourth weeks at 10° there was, in several cases, a further decline, the average food eaten per day for the fourth week amounting to 27 per cent of what it had been at 20°."

A rough correlation was found between mean monthly air temperatures (drawn from records of the United States Weather Bureau) and the time of annulus formation. This point will be discussed in the section on "Time of Annulus Formation."

Temperatures higher than the optimum for the species also tend to retard or stop growth. Audigè (1921) ascertained that certain temperate-zone fishes (*Cyprinus carpio, Carassius auratus,* and *Scardinius erythrophthalmus*) grew irregularly, with frequent checks, when held in water at 24–25° C. (75-77° F.) and that these checks were more pronounced at temperatures between 30° (86° F.) and 31° C. (87.8°F.). Similarly, it is known that the scales of tropical marine fishes often show annulus-like marks far too numerous to represent years. It is possible that the several annulus-like marks which formed in one year on the scales of some of the bluegills and largemouth bass in Fork Lake, Illinois (Bennett, Thompson, and Parr, 1940), were induced by the high summer temperatures, which led to a temporary cessation in growth. The weekly average water temperatures listed by these authors for the depth of three feet reached 85° F. (29° C.) for one week and remained over 75° F. (24° C.) for sixteen weeks from May 22 to September 18, 1939, with the exception of one week beginning June 12, when the mean temperature was 74° F. (23° C.). A collection made the following week (beginning June 19) exhibited the first accessory mark. Thus age determinations may be unreliable in shallow lakes where very high water temperatures occur over considerable periods.

Spawning

Spawning appears to have little effect on the time of annulus formation. The yellow perch spawn in early spring, but they form their annuli at about the same time as the late spawners. Johnston (1905, 1907), Taylor (1916), Morosov (1924), Hubbs and Cooper (1935), and others record that spawning marks, distinct from true annuli, are formed on scales. Many of the scales examined in this study exhibited accessory checks, which may be interpreted as spawning marks. These structures are most distinct on the anterior field. Further investigation is being carried on in an effort to determine the exact nature of these marks.

Food

Food has been considered of chief importance as a factor in annulus formation by Hoffbauer (1898, 1900), Thomson (1904), Fraser (1917), and Bhatia (1931). Van Oosten (1923), however, stated that

food is only a secondary factor in adults, but may be a primary factor in immature fish.

The author does not believe that food is often the primary factor. It has been shown by several workers (see discussion under "Temperature") that fish eat very little or no food at low temperatures, even when the supply is abundant. It would seem that temperature is more important than food as a factor directly controlling growth.

To be sure, if food is lacking, high temperatures would hardly be expected to induce the resumption of growth, which is essential in annulus formation. According to Hansen (1937), under certain conditions of malnutrition the white crappie (*Pomoxis annularis*), in Illinois, forms an absorption annulus that resembles the spawning mark which develops on the scales of salmon when they are spawning but not feeding. If the absorption of the scale can be taken as an indication of starvation, as Hansen suggested, the late formation of the annulus, found in these fish by Hansen, may well be attributed to a lack of food and a consequently long delay in the resumption of growth. This situation, however, is probably exceptional. The writer did not find any annuli of this absorption type on any of the thousands of scale samples of Michigan fishes.

It is possible also that the metamorphic or "natal" annulus of the Embiotocidae (Hubbs, 1921) is formed on a nutritional basis, for at birth the embryonic food supply is cut off, and retardation or even a temporary stoppage of growth may ensue before the young fish become adapted to the capture of the new type of food.

As Creaser (1926) emphasized, cessation and resumption of growth are the immediate factors involved in the formation of the annulus. Obviously, food can be a primary factor in annulus formation under those conditions in which these changes in growth are primarily determined by the supply of food organisms available.

TIME OF ANNULUS FORMATION

Few references to the time of annulus formation were made by the earlier workers on the age and growth of fishes. For the most part they were content to call the annulus the "winter mark" and apparently gave little consideration to the time of year at which the mark formed. A few men, however, directly or indirectly contributed data on this point.

Johnston (1905) found that the growth had begun at the end of

April on the scales of the salmon (*Salmo salar*) from the River Tay.

For the eel Gemzöe (1908) stated: "The growth of the scales begins in June, or, as a rule, first in July, and is ended at the end of September — sometimes (as in the silver eel) the growth ends somewhat earlier, seldom later."

The year mark was on the edge of the scales of the salmon taken in Ireland during January, February, and March, after which it was found within the edge in an increasing percentage. In May, June, and July collections from Norway the scales had the mark inside the edge in an increasing percentage, although some individual variation occurred (Dahl, 1911).

Lea (1911) showed that many of the herring scales collected on April 5-7 from waters near Bergen, Norway, had a small amount of new growth, whereas others taken at the same time did not. The fish of a sample taken on April 23 had formed new growth on the scales. Concerning Canadian collections, Lea subsequently stated (1919): "These later samples give a more definite idea as to the time when summer growth of the younger herring in these waters [off Prince Edward Island] begins, as in one of the samples (early June) the fish had not commenced their growth, while the remaining samples revealed a distinct new summer belt on the scales.

"An interesting feature in connection with these fish is the fact that summer growth commences so late. Off the coast of Norway, the new summer growth commences in April; but far up in the Baltic, near the coast of Finland, similar conditions are observed. Hellevaara . . ., who has investigated the herring of these waters, observes in this connection: 'Not until the 27th of June did I observe that the scales had begun to grow on the young fish 1 or 2 years old; but not on those which had reached maturity.'"

Sund (1911) found the location of the winter ring to be at the edge of the scales of the sprat (*Clupea sprattus*) taken in April, a short distance inside the margin in those collected in May, and again on the margin in a December sample. (It is doubtful, however, if the new annulus had formed in December).

In River Wye salmon Masterman (1913) discovered a marginal growth band of increasing width from April to September, but not in those taken in November and December.

The year mark is formed on the scales of the squeteague

(*Cynoscion regalis*) and pigfish (*Orthopristis chrysopterus*) in May or June (Taylor, 1916).

Fraser (1917) thus sums up his investigation: "In all scales of salmon [*Oncorhynchus tschawytscha*] caught from January 6 to March 17, there was indication of the check in growth at the margin. On the other hand, with but few exceptions, no scales obtained after April 22, and before November 27, had indication of retardation at the margin. From March 17 to April 22, and from November 27 to January 5, some show retardation at the margin while others do not, this being true even in specimens caught the same day." The author obviously did not distinguish the "dark band" of narrowed circuli from the true annulus. For the chinook salmon of the Columbia and Sacramento rivers Rich (1920) stated that growth is practically negligible from November to March, but more rapid growth is apparently resumed in April and May.

For the herring from the English Channel Hodgson (1925) showed that: "(1). The scales of English herring begin to grow during April and cease to grow in September, irrespective of their geographic position; (2). Younger fish have a longer growing period than older ones; (3). The older fish have a tendency to begin growth later than the younger fish." In Norwegian waters the scales of the herring had begun their growth in May (Lissner, 1925). In the haddock of Scottish waters Thompson (1926) found that the year mark always formed in March.

In 1941 Merriman stated: "Actually for the striped bass, the annulus does not appear in winter, and only becomes evident by April or May."

The papers mentioned above deal chiefly with ocean or river-run fish. Literature dealing with the time of annulus formation in freshwater fishes is also scanty. The following workers, however, have presented some data on the subject.

Van Oosten (1923) states that for the whitefish "the marginal growth is resumed sometime in April (or March?)." Creaser (1926) observed that "At Douglas Lake, Michigan, an investigation of the scales of many of the fishes showed that in June an annulus had only recently been formed."

For the bully (*Gobiomorphus gobioides*) in the Lower Selwyn River, South Island, New Zealand, Parrott (1934a) wrote: "It should be noticed that the summer annuli [wide circuli] are principally formed

during October, November, and December, while the winter annuli [narrow circuli] are formed principally during March, April, and May. There is, generally speaking, no growth in the scale during June, July, August, and September." He stated, further (1934b), that in the brown trout (*Salmo trutta*) the summer bands begins to develop in September and that by the end of October the majority show summer growth.

On the contrary, Hansen (1937) found that the annuli are formed over a long period in certain waters of Illinois. "In 1935 it was May, June, and July; in 1936, May, June, and possibly July."

According to Eschmeyer (1939), "Annulus formation in some of these immature fish [largemouth bass of Norris Reservoir, Tennessee] therefore extended over a long period, for a few had formed an annulus early in May and others had not begun growth by June 1, assuming that initial growth is reflected on the scale. . . . Two walleyes, taken late in March, had formed no annulus; 21 taken in late May and early June had made some growth; one caught in late May had not yet formed an annulus." In further studies on fish of the Norris Reservoir Jones (1941) determined that the growing season for the smallmouth and largemouth bass begins in June and ends early in October or late in September.

In a study mentioned on page 290 Bennett, Thompson, and Parr (1940) recorded the following observations: "Some of the yearling bluegills had formed annuli on their scales before April 18, and all of them had formed annuli by the end of May. Most breeder bluegills began annulus formation later than the yearlings, and did not complete this formation until October. Annulus formation in the bass extended from mid-April to late September."

For the white perch (*Morone americana*) Cooper (1941) stated that the growing season in Maine in 1940 extended from about the first or the second week in July through August and possibly through part of September.

Hile (1941) discarded a collection of old rock bass captured in Nebish Lake, Wisconsin, on July 5 and 6, 1930, because of his inability to decide whether certain individuals had formed the 1930 annulus. Annulus formation had been completed in the younger rock bass of a collection made July 1 and 2, 1932, in the neighboring Muskellunge Lake, but individuals of the same collection older than six years rarely exhibited a completed year mark.

The time of year at which the annulus forms in Michigan is distinctly earlier in the southern than in the northern part of the state. The extent of the difference is shown in Table II, where it may be seen that the year mark was formed and some marginal growth was evident on the scales of the fishes taken in the southern one third of the Lower Peninsula on May 17–20, 1940, whereas the scales of fish collected in the Upper Peninsula on May 22 had not yet begun to grow.

The statements of the following paragraphs in regard to the time of annulus formation in the different lakes apply to all species in each lake. (For details concerning species and the numbers in the collections see Appendix.) The lakes will be considered in the order in which they appear in Table II, with the exception of Pasinski Pond. The materials from this pond are of such a nature as to require a special discussion.

On some of the scales obtained from Clear Lake (Zone 1) on April 28, 1939, there was an annulus on the edge, and others had a trace of this mark. All those secured on June 1, 1939, when the lake was next fished, exhibited a completed annulus and a margin of new growth. The marginal annulus had formed on some of the scales taken on May 7, 1940, whereas on others there was only a trace or no indication at all of the year mark. The scales next collected here, on June 6, all showed an annulus well inside a margin of growth.

Data pertinent to the problem of the time of formation of the year mark were collected in Deep Lake (Zone 1) in connection with other investigations during 1939, and a special effort was made in 1940 and 1941 to take scale samples at frequent intervals. Certain aspects of these data have been discussed earlier (p. 291), in connection with the study of the factors of annulus formation.

None of the scales had a completed annulus in the first spring collection of April 27, 1939, although a few showed the beginning of one. There was no annulus on the scales taken on April 29. The next collection was made on May 17, at which time an annulus and a narrow band of growth were found on each scale.

In 1940 collections were begun on April 24. Samples taken then and on April 25, 29, 30, May 2, and May 8 had no annulus. On May 10 a few of the scales exhibited an annulus. On May 13–14 all but six of the samples had the year mark at the margin. Collections of May 20–22 showed the annulus within a narrow but distinct margin of growth.

TABLE II

TIME OF ANNULUS FORMATION ON THE SCALES OF GAME FISHES IN MICHIGAN

(See Appendix for details concerning the collections on which this table was based.)

Year	Zone	Lake	Dates when no scales had formed a marginal annulus		Dates when some scales had formed a marginal annulus			Dates when all scales had formed a marginal annulus	
			Date	Number of specimens	Date	Number of specimens		Date	Number of specimens
						with	without		
1939	1	Clear	Jan. 19 Feb. 25, 28	2 15	April 28 ...	7 ...	6 ...	June 1 July 15 Dec. 31	59 32 14
		Pasinski Pond	April 18 April 23	46 152	... ...	... ...	... ...	April 29 May 28 June 14–Oct. 12	38 69 327
		Deep	Feb. 2 April 27 April 29	2 8 5	... ...	... ...	... ...	May 17 May 19–31 June 2–Aug. 4	38 56 169
	2	Budd	...	...	May 17	59	14	June 19 Oct. 28	175 17
		Round	...	...	...	...	...	May 25 June 24 Oct. 20	15 77 7
	3	North Manistique	...	...	...	...	...	June 26 July 28 Sept. 7 Oct. 21	76 111 21 15

		Bass	...	...	...	...	...	June 25	16
								July 4	26
								July 29	72
								Sept. 15	6
								Oct. 22	16
		Crooked	...	...	...	...	...	July 1–3	68
								July 31	38
								Aug. 26	70
								Oct. 23	14
		Fannie Hooe	...	...	...	...	...	July 4–6	31
								Aug. 2–4	48
								Aug. 30	11
								Oct. 24	3
1940	1	Clear	...	...	May 7	13	31	June 6	53
		Deep	April 24, 25, 29, 30, May 2, 8	84	May 10	5	34	May 20	11
					May 13	37	3	May 22, 27,	
					May 14	21	3	June 14	68
	2	Budd	...	...	May 17	20	80	June 19	57
		Round	May 20	13	...	...	...	June 21, 22	50
	3	North Manistique	May 22, 23	53	...	...	...	June 24	28
								July 20, 21	49
		Bass	May 24	36	...	...	...	June 25	29
								July 23–24	59
		Crooked	May 26	30	...	...	...	June 26	17
								July 27	49
		Fannie Hooe	May 27–28	12	...	...	...	June 27	18
								July 27–29	39
1941	1	Deep	...	...	April 22	1	18	May 5	10
					April 24	12	39	May 7, 9, 12,	
					April 26	13	25	16, 19, 22, 24	66
					April 28	25	9		
					May 1	20	3		
					May 3	24	1		

The 1941 collections were begun on April 22, on which date only one bluegill revealed a marginal annulus. On April 24, 26, and 28, and May 1 and 3 increasing percentages of the scales had a marginal annulus. After May 3 all samples bore a marginal annulus with some growth beyond the annulus.

The annulus was just inside the edge on the majority of the scales of fish taken from Budd Lake (Zone 2), May 17–18, 1939, but only a few of those caught on May 17, 1940, had an annulus. All scales collected on June 19, 1939 and 1940, showed an annulus with a marginal growth.

On the scales secured in Round Lake (Zone 2) on May 26-28, 1939, the annulus was just inside the margin. In the next collection, made on June 21–23, an annulus was present within a wide band of growth on all fish. In 1940, scales collected on May 20 had no annulus, but all of those taken on June 19 exhibited an annulus inside the scale margin.

The annulus was on the edge of some scales collected in North Manistique Lake (Zone 3) on June 25, 1939, and a few scales had a slight marginal growth. In 1940 a collection made here on May 22 gave no indication that an annulus had been laid down. On June 24, when the next sample was obtained, the annulus had been formed on all specimens, with a slight marginal growth on some.

In Bass Lake (Zone 3) the annulus was obvious on all specimens when a collection was made on June 25, 1939. All scales taken on July 28–29 showed a band of marginal growth that was distinctly wider than that on the scales of the previous collection. In 1940 a sample was taken on May 24, at which time no annulus was apparent. When the next collection was made, on June 25, the annulus had formed on all scales.

Collections were made on July 1–3, 1939, in Crooked Lake (Zone 3). The annulus was to be seen on the edge of the scales. In 1940 a collection made in May showed no annulus present. All scales collected on June 26, 1940, had an annulus near the edge.

On the scale samples secured from Lake Fannie Hooe (Zone 3) on July 4–6, 1939, the annulus was just inside the edge of all except a few, which had a fair amount of marginal growth. No annulus was present on any of the scales collected on May 27–28, 1940. The next collection, taken on June 27–28, showed an annulus near the edge of all scales.

Additional scattered material was obtained through samples of scales taken in the springs of 1939 and 1940 from other lakes that were visited during the investigation of other problems. Others were obtained from Standard Lake (Zone 2) during May and June, 1939, and from Ford Lake (Zone 2) in May, 1939, and May, 1940. Samples were kept from fish caught in June, 1940, during a survey of certain lakes in Menominee County (Zone 3). In all these samples the indicated time of annulus formation agreed with the findings for the selected lakes in the same region.

The data on the bluegills of Pasinski Pond not only provide information concerning the time of annulus formation but also yield strong evidence in support of the belief that only one annulus is formed each year. The annulus formed on the scales of bluegills (the only game fish present) in the pond (Zone 1) between April 23 and 29, 1939. None of the scales collected on April 23 had a marginal annulus, but the year mark was evident on the scales of all fish taken on April 29. It was impossible to continue the observations here beyond the growing season of 1939 because this pond suffered a complete winterkill in February, 1940. This event was particularly unfortunate since the fish were of known age and many had been jaw-tagged.

The second-year growth of these fish (all known to be yearlings) up to different times of capture in the growing season is described as the percentages of the average "expected" growth for the entire growing season of 1939. This average full-season growth, derived from the measurements of the scales of 164 bluegills taken at the time of the winterkill is indicated by the heavy vertical line on the graph (Fig. 2). The range of length and the number of specimens on which each percentage is based are shown by the frequency curves. The mean growth of each collection is represented by a broken vertical line.

It will be seen that on April 23 no fish had an annulus, but an annulus with a small amount of marginal growth was present in all specimens in the collection of April 29. A steady increase in the percentage of the annual growth completed occurred in the succeeding collections. Though the range of variation increased somewhat during the season, none of the fish taken in May, June, or July had the annulus sufficiently close to the margin to indicate recent formation. By July approximately 85 per cent of the "expected" growth for

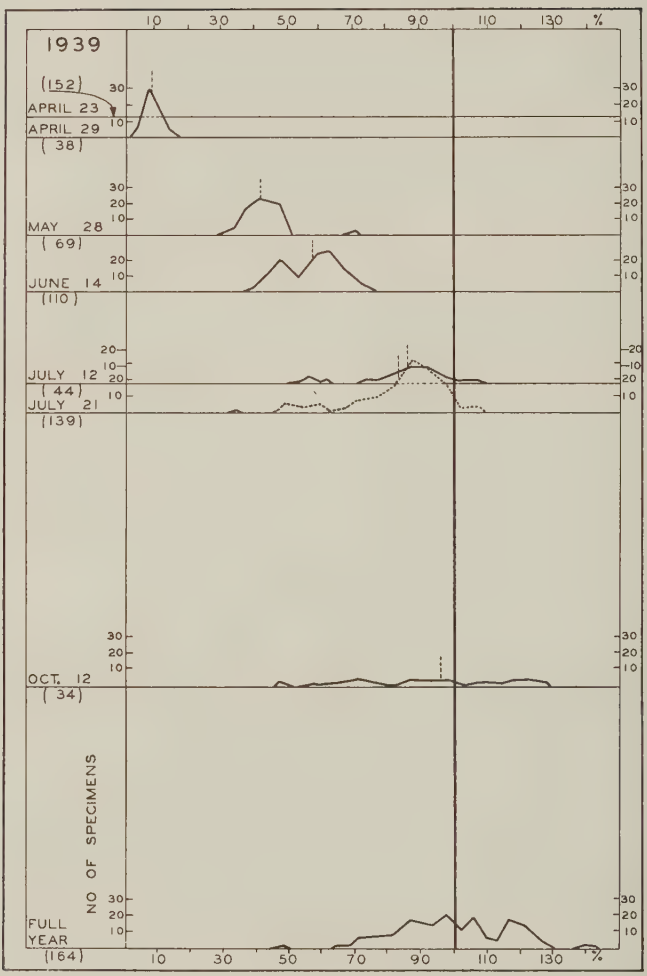

FIG. 2. Percentage of "expected" annual scale growth completed on different dates by yearling bluegills from Pasinski Pond in 1939. Number of specimens in parentheses. Heavy solid line indicates the mean of the full year's growth. Broken lines indicate the means of the individual collections

the season had been completed. In October a small collection showed that 96 per cent of the "expected" growth had been attained. When the fish were killed in February, 1940, they had not yet formed the second annulus, but undoubtedly would have completed this structure in the spring had they lived.

The relatively small variation in the amount of the marginal growth on the scales of the Pasinski Pond bluegills caught on the same date and the increase of this growth during the summer are illustrated by the photographs in Plates II–IV. The scales that are pictured were taken at random from the collections of the dates listed.

The data for other waters as well as for Pasinski Pond indicate uniformly that only one annulus is formed each year. For a number of species and in several lakes the relative amounts of the annual scale growth outside the marginal annulus were calculated for each date of sampling. Table III shows the typical results of the calculations. The amount of growth at any date is given as the percentage of the "expected" full-season growth for fish in that particular year of life. The "expected" annual scale growth was determined as the mean of the full-season increments of the scale for each year of life for all specimens that had survived beyond that year. For example, the average scale growth for the first year of life was based on the growth made in that year by all fish in the collection one year old and older, and that for the second year was based on all fish two years old and older, and so on. The percentage of scale growth completed at the time of capture was obtained by dividing the average growth outside the annulus by the average full-season growth expected for fish in the same year of life. The table shows that the annulus formed between certain dates and that in successive collections lay farther and farther within the scale margin. It may be seen also from Table III that in Deep Lake, as in Pasinski Pond, all annuli were completed within a very short period. It is believed that the annulus forms rapidly in all lakes.

The time of annulus formation is correlated roughly with the mean monthly air temperatures. At comparable dates the springs of 1939 and 1941 were warmer than the spring of 1940, and the annulus formed earlier in 1939 and 1941 than in 1940. Since water temperature and air temperature are correlated rather closely, it is to be expected that the water would become warmer earlier in a warm

TABLE III

SCALE GROWTH OUTSIDE MARGINAL ANNULUS, AS THE PERCENTAGE OF THE EXPECTED TOTAL GROWTH FOR THE GIVEN YEAR

The average expected scale growth for a particular year of life was based on average measurements of the scale growth of all fish that had completed that year of life. The data are based on collections from Deep Lake.

Species and date	Age group						
	I	II	III	IV	V	VI	VII
Bluegill							
February 4, 1939	...	...	...	...	0 (2)	...	...
April 27, 29	...	...	...	0 (2)	0 (5)	...	...
May 17, 19, 21, 27	...	...	17 (10)	20 (25)	33 (14)	44 (1)	...
June 5, 8, 13, 20, 28	...	25 (1)	35 (17)	38 (27)	40 (9)	...	...
July 2, 5, 7, 13, 24, 26	44 (2)	47 (15)	57 (10)	51 (17)	61 (3)	...	...
August 2, 4	...	78 (1)	78 (3)	64 (6)	...	...	...
April 29, 1940	...	...	0 (1)	...	...	...	...
May 2, 8	...	...	0 (4)	0 (3)	...	...	...
May 10	...	0 (2)	*0.8 (6)	0 (2)	...	...	...
May 13, 14	...	...	5 (11)	7 (5)	13 (7)	12 (6)	0 (1)
May 20, 22, 27	...	...	...	15 (5)	24 (5)	35 (3)	...
June 14	115 (2)	37 (5)	30 (12)	32 (2)	44 (1)	...	...
Pumpkinseed							
April 27, 1939	...	...	...	...	0 (1)	...	...
May 17, 21, 27	...	...	...	...	27 (20)	...	...
June 5, 8, 13, 20, 28	...	...	...	...	53 (7)	...	...
July 2, 12, 13, 24	62 (3)	51 (10)	50 (2)	62 (5)	103 (2)	...	...
August 2	...	...	...	...	77 (2)	...	...
April 25, 29, 30, 1940	...	...	0 (7)	0 (5)	0 (4)	0 (4)	...
May 2, 8	...	...	0 (6)	0 (4)	0 (9)	0 (4)	0 (1)
May 10	...	...	*1 (2)	*3 (2)	...	...	0 (1)
May 13, 14	...	...	*10 (7)	13 (5)	4 (1)	...	...
May 20, 22, 27	...	...	27 (2)	34 (4)	36 (3)	...	...
June 14	...	38 (2)	49 (15)	54 (1)	...	...	...

* Some with or without growth

spring than in a cold one. When the lakes of the southern part of the Lower Peninsula have become sufficiently warm to permit the resumption of fish growth, the lakes in the Upper Peninsula are barely ice-free. As the temperatures gradually increase in the north, growth of the fish in these lakes is finally resumed, with the resultant annulus formation. Since the local temperature conditions vary

considerably from year to year, and since the isotherms form irregular patterns, it was found impracticable to delimit on the basis of isotherms the zones or sections which are needed for a further analysis of the variations throughout the state in the time of annulus formation. The lines of separation of three general areas or zones were set somewhat arbitrarily as Town Line 10 North and the Straits of Mackinac. Zone 1 extends from the southern boundary of the state north to Town Line 10; Zone 2 covers the Lower Peninsula north of this line; and Zone 3 comprises the entire Upper Peninsula (Fig. 1). It must be remembered that the temperatures decrease gradually toward the north, and it has been found that the time of annulus formation shows a similar gradient, without the abrupt discontinuities that zones are likely to suggest.

It is estimated that in an "average" year the annulus is usually completed in Zone 1, the southern one third of the Lower Peninsula, by the middle of May; in Zone 2, the northern two thirds of the Lower Peninsula, by the first part of June; and in Zone 3, the Upper Peninsula, by the end of June. The date of actual completion will vary somewhat according to temperature conditions in different localities and in different years.

SUMMARY

1. The investigation of annulus formation on the scales of some of the game fishes of Michigan was begun in 1939 under the sponsorship of the Michigan Institute for Fisheries Research.

2. Scale samples were collected at regular intervals from seven lakes and a pond; additional samples were taken from other lakes in connection with other investigations.

3. Temperature appears to be the primary factor in annulus formation.

4. Spawning was found to have little or no effect on the time of annulus formation.

5. Food is ordinarily of secondary importance as a factor in the time of annulus formation. A severe scarcity of food, or an abrupt change in the availability of food, may make it a primary factor.

6. The mean temperatures of the days on which the scales in the collections first showed annuli were 53° F. in 1940 and 52° F. in 1941. The mean temperatures of the first days on which the majority of the scale samples showed an annulus were 58° F. in both 1940 and 1941.

7. The annulus formed earlier in 1939 and 1941 than in 1940. The earlier formation in 1939 and 1941 was correlated with the higher temperatures at corresponding dates in those two years.

8. The time of annulus formation was progressively later from the southern part of Michigan to the northern part.

9. The state was divided arbitrarily into three zones: Zone 1, roughly the southern one third of the Lower Peninsula; Zone 2, the northern two thirds of the Lower Peninsula; and Zone 3, the Upper Peninsula. In all but exceptionally cold years the formation of the annulus may be expected to be completed in Zone 1 by the middle of May; in Zone 2, by the first part of June; and in Zone 3, by the end of June. Annual fluctuations in temperature may bring about some variation in the date of formation of the year mark.

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APPENDIX

Detailed Data on the Time of Annulus Formation on the Scales of Michigan Game Fishes

The data of Table III on the time of annulus formation on the scales of Michigan game fishes are not presented by species. The following data show definitely that the different species formed the year mark simultaneously as they started to grow in the spring.

CLEAR LAKE, JACKSON COUNTY

Data for 1939

Annulus not yet formed at the margin:
January 19: 2 black crappies
February 25, 28: 15 bluegills
Marginal annulus formed in some specimens:
April 28: 6 perch with annuli, 2 without; 2 bluegills without; 1 rock bass without; 1 black crappie with, 1 without
Annulus formed on all scales:
June 1: 12 perch, 6 largemouth bass, 19 bluegills, 2 rock bass, 16 pumpkinseeds, 4 black crappies
July 15: 6 perch, 5 largemouth bass, 13 bluegills, 8 pumpkinseeds
December 31: 6 bluegills, 8 black crappies

Data for 1940

Marginal annulus formed in some specimens:
May 7: 3 largemouth bass without annuli; 2 bluegills with, 22 without; 10 pumpkinseeds with, 4 without; 1 green sunfish × bluegill with, 2 without
Annulus formed on all scales:
June 6: 17 perch, 6 largemouth bass, 9 bluegills, 9 rock bass, 6 pumpkinseeds, 4 black crappies, 2 green sunfish

BUDD LAKE, CLARE COUNTY

Data for 1939

Marginal annulus formed in some specimens:
May 17: 21 perch with annuli, 9 without; 24 bluegills with; 5 pumpkinseeds with, 4 without; 3 largemouth bass with, 1 without; 2 rock bass with; 1 black crappie with; 3 pumpkinseed × green sunfish with
Annulus formed on all scales:
June 19: 52 perch, 29 bluegills, 70 pumpkinseeds, 13 largemouth bass, 1 green sunfish, 4 rock bass, 3 black crappies, 2 bluegill × pumpkinseed, 1 pumpkinseed × green sunfish
October 28: 1 perch, 3 bluegills, 6 pumpkinseeds, 2 largemouth bass, 5 rock bass

Data for 1940

Marginal annulus formed in some specimens:
May 17: 7 perch with annuli, 20 without; 1 bluegill with, 31 without; 3 pumpkinseeds with, 5 without; 6 largemouth bass without; 1 green sunfish without; 9 rock bass with, 10 without; 2 black crappies without; 5 pumpkinseed × green sunfish without
Annulus formed on all scales:
June 19: 14 perch, 16 bluegills, 15 pumpkinseeds, 8 largemouth bass, 1 green sunfish, 3 rock bass

ROUND LAKE, EMMET COUNTY

Data for 1939

Annulus formed on all scales:
May 25:. 10 pumpkinseeds, 5 rock bass
June 24: 25 pumpkinseeds, 19 bluegills, 21 perch, 12 rock bass
October 20: 1 pumpkinseed, 3 bluegills, 2 rock bass, 1 largemouth bass

Data for 1940

Annulus not yet formed at margin:
May 20: 6 pumpkinseeds, 4 rock bass, 3 largemouth bass
Annulus formed on all scales:
June 21: 22 pumpkinseeds, 18 bluegills, 2 perch, 7 rock bass, 1 largemouth bass

NORTH MANISTIQUE LAKE, LUCE COUNTY

Data for 1939

Annulus formed on all scales:
June 26: 32 rock bass, 27 perch, 9 walleyes, 8 smallmouth bass
July 28: 43 rock bass, 61 perch, 6 walleyes, 1 smallmouth bass
September 7: 5 rock bass, 8 perch, 8 walleyes
October 21: 2 rock bass, 7 perch, 6 walleyes

Data for 1940

Annulus not yet formed at margin:
May 23: 28 rock bass, 18 perch, 7 walleyes
Annulus formed on all scales:
June 24: 8 rock bass, 16 perch, 4 walleyes
July 21: 16 rock bass, 21 perch, 6 walleyes, 6 smallmouth bass

BASS LAKE, MARQUETTE COUNTY

Data for 1939

Annulus formed on all scales:
June 25: 14 pumpkinseeds, 2 pumpkinseed × bluegill
July 4: 8 bluegills, 16 pumpkinseeds, 1 perch
July 29: 41 bluegills, 19 pumpkinseeds, 6 perch, 3 walleyes, 3 largemouth bass
September 15: 3 bluegills, 1 pumpkinseed, 2 walleyes
October 22: 8 bluegills, 6 perch, 1 largemouth bass, 1 smallmouth bass

Data for 1940

Annulus not yet formed at margin:
May 24: 17 bluegills, 10 pumpkinseeds, 4 perch, 1 walleye, 3 largemouth bass, 1 smallmouth bass
Annulus formed on all scales:
June 25: 10 bluegills, 7 pumpkinseeds, 5 perch, 6 walleyes, 1 largemouth bass
July 24: 30 bluegills, 7 pumpkinseeds, 18 perch, 2 walleyes, 1 largemouth bass, 1 smallmouth bass

CROOKED LAKE, GOGEBIC COUNTY

Data for 1939

Annulus formed on all scales:
July 3: 32 perch, 11 bluegills, 9 smallmouth bass, 5 largemouth bass, 2 black crappies, 9 pumpkinseeds
July 31: 16 perch, 4 bluegills, 9 smallmouth bass, 6 largemouth bass, 1 black crappie, 2 pumpkinseeds
August 26: 54 perch, 8 bluegills, 1 smallmouth bass, 6 largemouth bass, 1 black crappie
October 23: 9 perch, 2 bluegills, 2 smallmouth bass, 1 pumpkinseed

Data for 1940

Annulus not yet formed at margin:
May 26: 22 perch, 1 bluegill, 1 smallmouth bass, 6 black crappies
Annulus formed on all scales:
June 27: 15 perch, 2 bluegills
July 27: 38 perch, 6 bluegills, 3 largemouth bass, 2 black crappies

LAKE FANNIE HOOE, KEWEENAW COUNTY

Data for 1939

Annulus formed on all scales:
July 4–6: 19 rock bass, 8 perch, 3 smallmouth bass, 1 bluegill
August 2–4: 21 rock bass, 27 perch
August 30: 4 rock bass, 7 perch
October 24: 1 rock bass, 1 perch

Data for 1940

Annulus not yet formed at margin:
May 27–28: 4 rock bass, 7 perch, 1 bluegill
Annulus formed on all scales:
June 27: 10 rock bass, 8 perch
July 27–29: 19 rock bass, 20 perch

DEEP LAKE, OAKLAND COUNTY

Data for 1939

Annulus not yet formed on margin:
February 2: 2 bluegills
April 27: 5 rock bass, 1 pumpkinseed, 2 bluegills
April 29: 5 bluegills
Annulus formed on all scales:
May 17: 14 rock bass, 15 pumpkinseeds, 9 bluegills
May 19: 1 pumpkinseed, 2 bluegills
May 21: 1 rock bass, 1 pumpkinseed, 20 bluegills
May, June, July, August: 10 rock bass, 46 pumpkinseeds, 144 bluegills

Data for 1940

Annulus not yet formed at margin:
April 24: 1 rock bass
April 25: 1 pumpkinseed
April 29: 7 rock bass, 4 pumpkinseeds, 1 bluegill
April 30: 2 rock bass, 15 pumpkinseeds, 2 largemouth bass
May 2: 5 rock bass, 16 pumpkinseeds, 3 bluegills, 2 largemouth bass
May 8: 16 rock bass, 7 pumpkinseeds, 4 bluegills
Marginal annulus formed in some specimens:
May 10: 2 rock bass with annuli, 14 without; 2 pumpkinseeds with, 11 without; 1 bluegill with, 9 without; 1 largemouth bass without
May 13: 7 rock bass with annuli, 1 without; 8 pumpkinseeds with; 22 bluegills with, 2 without

May 14: 7 rock bass with annuli, 1 without; 7 pumpkinseeds with, 1 without; 7 bluegills with, 1 without

Annulus formed on all scales:

May 20: 4 rock bass, 2 pumpkinseeds, 5 bluegills
May 22: 1 rock bass, 4 pumpkinseeds, 9 bluegills
May 27: 1 rock bass, 4 pumpkinseeds, 2 bluegills, 2 largemouth bass
June 14: 5 rock bass, 18 pumpkinseeds, 22 bluegills

Data for 1941

Marginal annulus formed in some specimens:

April 22: 2 pumpkinseeds without annuli; 1 bluegill with, 16 without
April 24: 2 rock bass with annuli, 8 without; 6 pumpkinseeds with, 17 without; 4 bluegills with, 14 without
April 26: 5 pumpkinseeds with annuli, 9 without; 8 bluegills with, 16 without
April 28: 5 rock bass with annuli; 8 pumpkinseeds with, 5 without; 12 bluegills with, 4 without
May 1: 3 rock bass with annuli; 11 pumpkinseeds with, 2 without; 6 bluegills with, 1 without
May 3: 4 rock bass with annuli; 11 pumpkinseeds with; 9 bluegills with, 1 without

Annulus formed on all scales:

May 5: 2 rock bass, 5 pumpkinseeds, 3 bluegills
May 7: 2 rock bass, 4 pumpkinseeds, 2 bluegills
May 9: 1 rock bass, 2 bluegills
May 12: 2 rock bass, 4 pumpkinseeds, 2 bluegills
May 16–24: 7 rock bass, 17 pumpkinseeds, 23 bluegills

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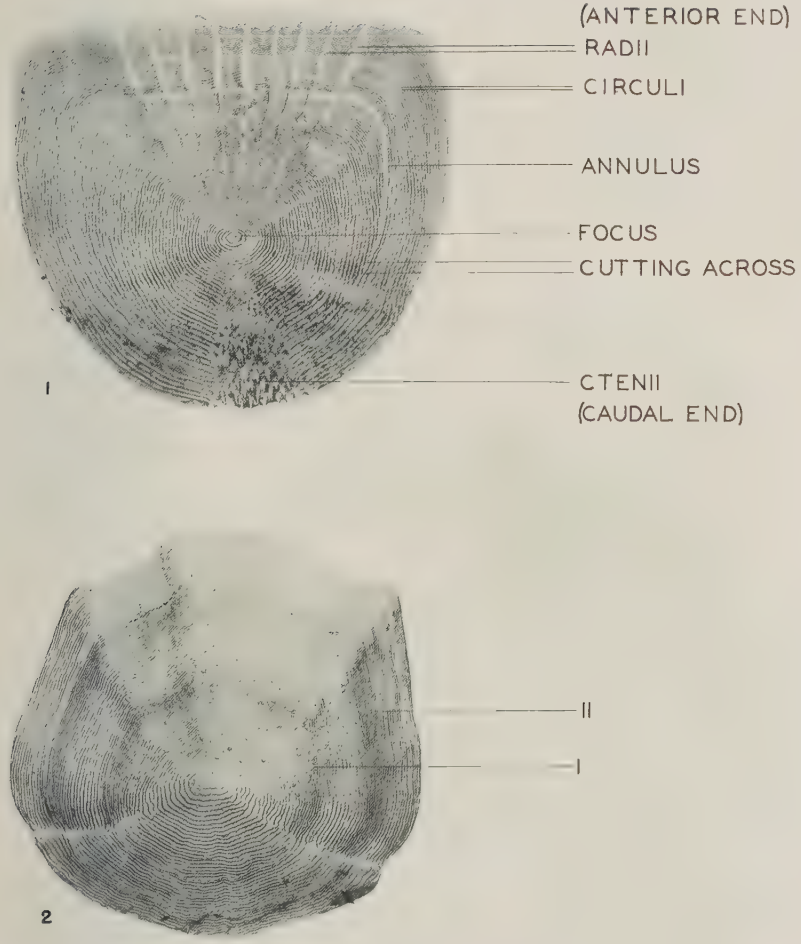
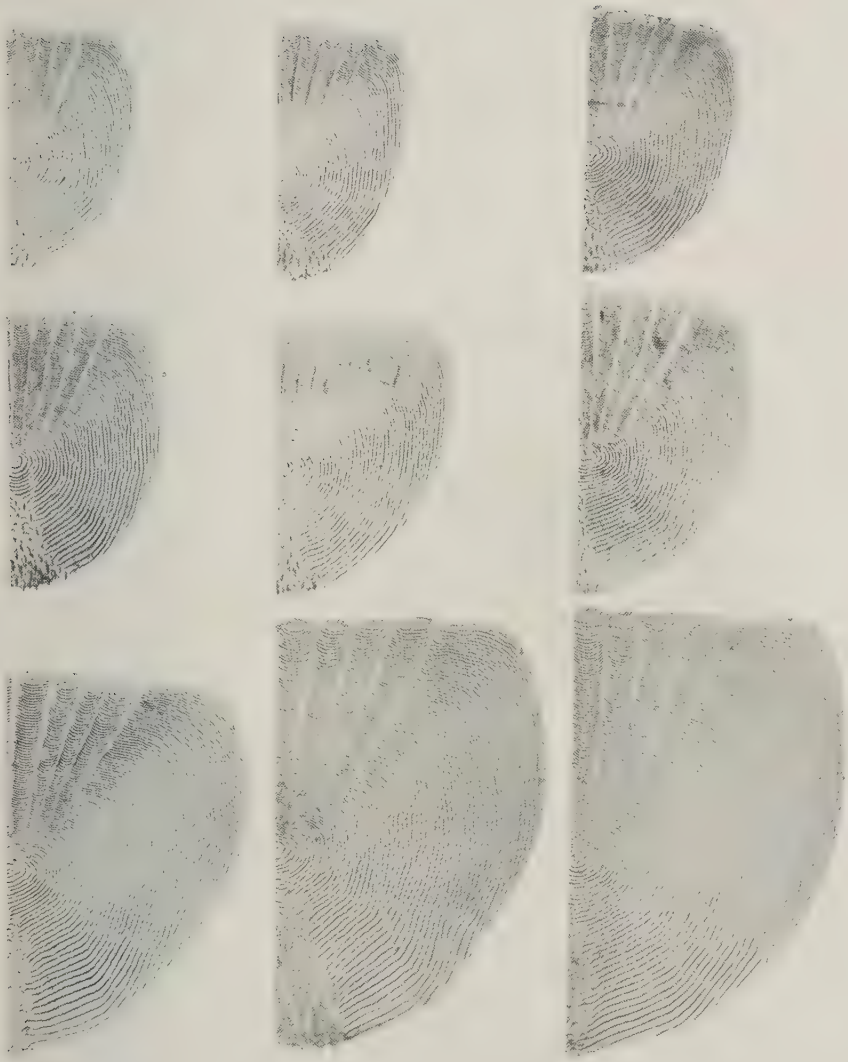
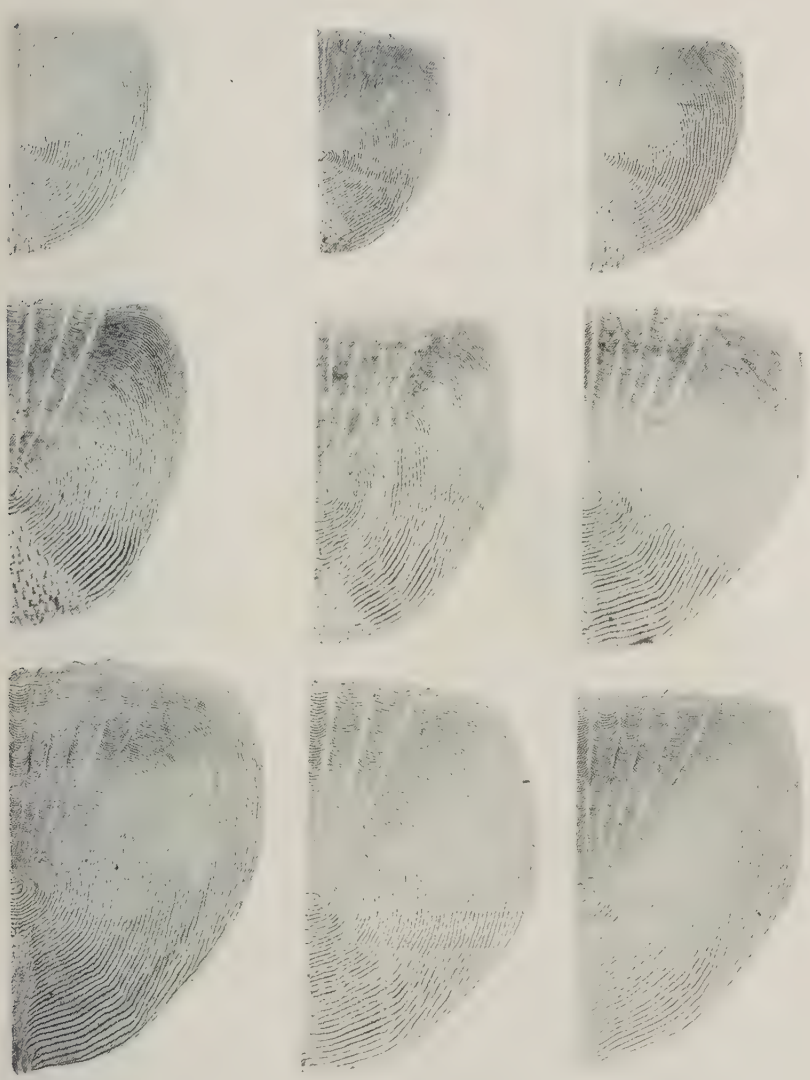


Fig. 1. Ctenoid scale from a bluegill $4\frac{1}{4}$ inches long. Age one year
Fig. 2. Cycloid scale from a cisco 11 inches long. Age two years
(Annuli indicated by Roman numerals)

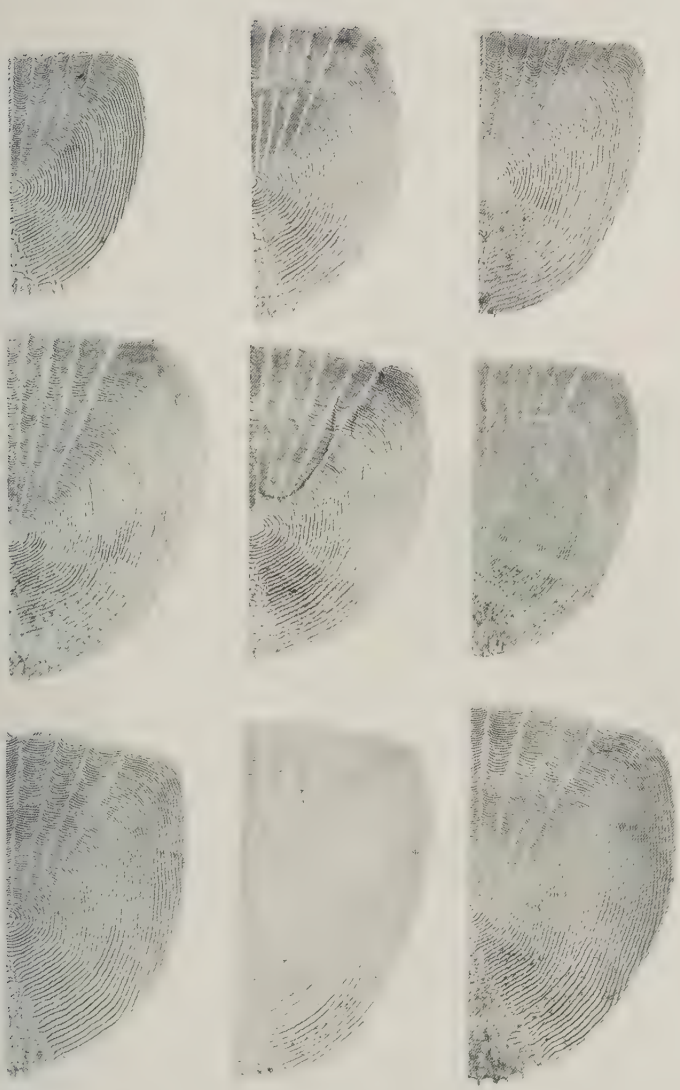


Scales of bluegills (size range, $2\frac{7}{8}$–$4\frac{1}{4}$ inches, total length) taken from Pasinski Pond, Livingston County, Michigan, April 23, 1939. No annulus present.

(All photographs in Plates II IV taken at a magnification of 44.3)



Scales of bluegills (size range, $2\frac{3}{4}$–$4\frac{1}{4}$ inches, total length) taken from Pasinski Pond April 29, 1939. Annulus at edge



Scales of bluegills (size range, $2\frac{3}{4}$–$4\frac{1}{4}$ inches, total length) taken from Pasinski Pond, June 14, 1939. Annulus well inside margin of growth

A TEST OF FECUNDITY OF THE GARTER SNAKE *THAMNOPHIS SIRTALIS SIRTALIS* (LINNAEUS) IN THE YEAR FOLLOWING THE YEAR OF INSEMINATION *

FRIEDA COBB BLANCHARD

IN THE routine of my genetical studies of the garter snake *Thamnophis sirtalis sirtalis* a female has been regarded as safe material for controlled mating in the spring if she has been isolated from males since before the birth of her brood in the preceding summer. The technique has been based on the supposition that sperm do not live in the female from one spring to the next, that one insemination does not produce two broods, in successive years.

There is good evidence that some females caught in the fall are already impregnated and may bear young in the following summer without a spring mating [1] — that is, that sperm or embryos may hibernate within the female — yet in the work of many years no reason has been seen for believing that two broods, a year apart, could result from one insemination. In the earlier years of the work it happened more than a dozen times that a female which had young one summer did not mate in the following spring, and each time she was barren. In no instance was a female which was isolated previous to the birth of her young known to have another brood without another copulation. But because these instances were scattered through the years and the females involved were heterogeneous if considered as a group, and because of the doubts cast on breeding data as a result of the recent discovery of "delayed fertilization" in some snakes, a planned test of fecundity in the second year was made.

* Paper No. 805 from the Botanical Garden and the Department of Botany of the University of Michigan.

[1] Blanchard, F. N. and Frieda Cobb, "The Inheritance of Melanism in the Garter Snake *Thamnophis sirtalis sirtalis* (Linnaeus), and Some Evidence of Effective Autumn Mating," *Pap. Mich. Acad. Sci., Arts, and Letters*, 26 (1940): 177–193. 1941.

Thirty-five females which had been caught and isolated shortly before their young were born in the summer of 1940 were continued in isolation during the following year, 1941. Of the thirty-five, seventeen came from the vicinity of Cheboygan, Michigan, twelve from Long Point, Ontario, and the other six were of various local origins. In length they ranged from 660 mm. to 930 mm.; only seven were under 700 mm. This group of females, isolated since before the birth of their young in the summer of the preceding year, proved to be entirely barren in 1941. There is of course a remote possibility that in each of the thirty-five instances the 1940 brood itself was the second of two broods following a single insemination in the spring of 1939; but this is extremely unlikely. The test seems to give good evidence that in *Thamnophis sirtalis sirtalis* two broods are not produced by a single insemination and that females isolated before the birth of their young may safely be used at any time thereafter for controlled mating.

Although females have been known to produce young after a spring in which no mating occurred, presumably from an insemination of the preceding autumn, nothing has been known about the frequency of effectual autumn mating in nature. With this question in mind, an attempt was made in October, 1940, to catch females just before their hibernation, when they had had all possible chance for fall mating. Eight females caught at Long Point during the first two weeks of October, 1940, were kept in isolation until autumn of 1941. Of the eight, five bore young, and three (which were small, but probably mature) did not. This ratio indicates that autumn mating is common, perhaps usual.

Whether or not fall mating influences or obviates mating in the following spring has not been determined, but the ratios of color patterns (black and striped) in the five broods just mentioned throw some light on this matter, and at the same time help to explain the odd color ratios recorded by Logier [2] in broods of wild females at Long Point. Though melanism is a simple Mendelian recessive character,[3] the broods borne by black females which mate in the wild give ratios of striped to black snakelings which do not even suggest Mendelian ratios: in a mixed brood there may be only one

[2] Logier, E. B. S., "Melanism in the Garter Snake, *Thamnophis sirtalis sirtalis*, in Ontario," *Copeia*, 172: 83–84. 1929; "Some Additional Notes on Melanism in *Thamnophis sirtalis sirtalis* in Ontario," *Copeia*, 1: 20. 1930.

[3] See Blanchard and Blanchard, *op. cit.*

black among the striped snakelings, or they may all be black except one, or there may be any ratio between these extremes. In explanation of this odd circumstance it has been suggested that the females mate more than once, and that a brood may represent more than one male, for, unless the males happened to be alike in genetical constitution, this would result in quite irregular ratios, like those which actually occur. But in the spring, females under observation seem to avoid more than one copulation (or perhaps the males avoid courting a female recently impregnated). Therefore it has been suggested (without supporting observations) that the wild females may mate in the autumn and again in the spring, thus producing broods with meaningless, irregular ratios.

If the irregular ratios do result from an autumn mating followed by another in the spring, females caught after opportunity for fall insemination and prevented from mating in the spring might be expected to bear broods showing Mendelian segregation; and this is what happened in the five instances just mentioned. One of the five females was black, and her progeny were all black, indicating that her mate also was black. Of the four striped females, two gave broods entirely of striped young, showing that each was homozygous for the factor for stripe or, if heterozygous, that the male involved was homozygous. The other two striped females gave mixed broods, the ratio of striped to black young (3 striped : 5 black; 4 striped : 3 black) being sufficiently close to a 1 : 1 ratio to indicate that both females were heterozygous and mated with a black male. These five broods, therefore, not only show the prevalence of mating in the fall, but indicate that in nature this does not interfere with spring mating, and support the belief that the confused color ratios in wild broods are the result of an autumn mating followed by one in the spring.

If the preceding explanation of irregular color ratios is correct (that a brood may represent two males, one copulating in the autumn, the other in the spring), it is evident that though insemination may occur in the fall the eggs are not fertilized until after the spring insemination. That sperm, rather than embryos, hibernate within the female is indicated also by the fact that the five broods resulting from mating in the autumn, without subsequent spring mating, were not born earlier in the following summer than were broods from spring copulations.

SUMMARY

1. That young are not produced in successive summers by a single insemination is shown by the fact that no broods were borne in 1941 by thirty-five females which were caught and isolated before their young were born in 1940.

2. That effective autumn mating is common in nature is shown by the fact that five out of eight females caught and isolated in October, 1940, produced broods in the summer of 1941 without spring mating. The three which were barren were small but probably mature.

3. The broods borne by these five females, caught at Long Point, Ontario, in the fall, showed Mendelian ratios of striped and black young, though the broods of females caught in spring at the same place do not. This supports the suggestion that the irregular ratios in nature result from two copulations, that in the spring being preceded by one in the fall.

4. If this is the correct explanation of the irregular color ratios in nature, it follows that though insemination may take place in the fall, fertilization does not occur until spring. This is indicated also by the fact that the five broods from fall matings alone were not born earlier than broods from matings of the following spring.

University of Michigan

FEMALE ALLOTYPE OF *LANDANA SPINOSA* PETRUNKEVITCH

ARTHUR M. CHICKERING

WHILE conducting field studies on Barro Colorado Island, Canal Zone, in August, 1938, Dr. Alexander Petrunkevitch collected two male specimens of a very remarkable species. He made one of these spiders the type of *Landana spinosa* (1939) and extended his study to include internal anatomy. Examination of the internal and external anatomy of these specimens led Dr. Petrunkevitch to reinvestigate the anatomy of specimens of *Archaea workmanni* (O. P. Cambridge) from Madagascar. This further led to the reconsideration of the status of the family Archaeidae and the reassignment of *Landana* to this family, where it was originally placed by Simon (1883). On the basis of marked differences in structure between the sexes in *Landana* and the fact that *L. cygnea* builds geometric orb webs, Simon later (1895) placed the genus among the Argiopidae, near *Meta*.

I collected both sexes of *Landana spinosa* Petrunkevitch on Barro Colorado Island, Canal Zone, in 1934, 1936, and 1939. The males were assigned to the genus *Landana*, but they were not carefully studied at that time. The females were wrongly assigned to a genus in the Argiopidae. These have now been definitely matched up with the males, and one is described below as the allotype. Soon after the publication of Petrunkevitch's paper (1939) on *Landana* I sent specimens of my females to Miss Elizabeth B. Bryant, Museum of Comparative Zoölogy, Harvard College, for her opinion regarding their placement. Miss Bryant almost immediately recognized them as females of *L. spinosa*.

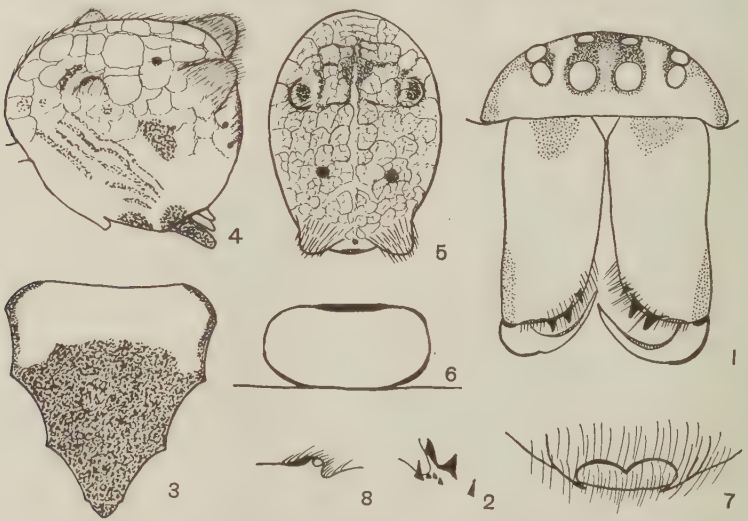
DIAGNOSIS

(Figures 1–8)

Female allotype. — Total length from posterior abdominal humps to anterior end of cephalothorax 4.16 mm. Carapace 1.96 mm. long, 1.35 mm. wide at widest part between second and third coxae, 0.73

mm. wide at level of posterior eyes. Thoracic groove lacking, but in its place a transverse depression. Head and thorax well separated by cephalic grooves. Gently arched from posterior eyes to cephalic depression.

Eyes. — Eight in two rows, heterogeneous (Fig. 1); AME alone diurnal. Two rows of almost equal length. Seen from above, posterior row slightly procurved, anterior row strongly recurved. Ratio of



EXTERNAL ANATOMY OF *LANDANA SPINOSA* PETRUNKEVITCH

(Figures 1–8)

1. Front view of chelicerae, eyes, and clypeus
2. Teeth along margins of fang groove
3. Sternum
4. Abdomen, lateral view
5. Abdomen, dorsal view
6. Epigynum, viewed somewhat posteriorly
7. Epigynum, viewed ventrally
8. Epigynum, in profile

eyes AME : ALE : PME : PLE = 4 : 3 : 3 : 3. AME separated from one another by their diameter, from ALE by their diameter. PME separated from one another by their diameter, from PLE by twice their diameter. Laterals separated by a line. Central ocular quad-

rangle wider in front than behind in ratio of 11 : 9, longer than wide in front in ratio of 13.5 : 11. Width of clypeus a little greater than diameter of AME.

Chelicerae. — Of normal size, slightly gibbous in front at proximal end just below clypeus, basal segment 0.94 mm. long, with a moderately developed boss, insertion apparently normal. Promargin of fang groove with three teeth of moderate size, the last two next to base of fang connected at their bases; retromargin with one tooth of moderate size near base of fang, followed by a row of three minute teeth out of line (Figs. 1–2). A paratype has four of these minute teeth. Fang of moderate size and evenly curved.

Maxillae. — Longer than wide in ratio of 20 : 14, widest near distal end, nearly parallel, with well-developed scopulae along medial borders and inner distal angle; well-developed marginal serrulae; rostrum not abnormally long as described for male; nearly straight outer margins.

Lip. — Wider than long in ratio of 12 : 9, distal margin somewhat rebordered and gently curved, reaches less than half the length of maxillae.

Sternum. — Scutiform, longer than wide in ratio of 31 : 27, widest between intervals separating first and second coxae, with many long bristles, extending to a blunt termination between posterior coxae, which are separated by their radius (Fig. 3).

Legs. — 1243. Tibial index of first leg 10, of fourth leg 15.

	Femora	*Patellae and tibiae*	*Metatarsi*	*Tarsi*	*Totals*
	(All measurements in millimeters)				
1.	2.66	2.82	2.10	0.86	8.44
2.	2.08	2.32	1.59	0.70	6.69
3.	1.23	1.22	0.68	0.48	3.61
4.	1.96	1.59	1.08	0.49	5.12

Spines. — First leg: femur, dorsal 1 (weak) – 0 – 0, prolateral 0 – 1 – 1 (weak) – 1, retrolateral 0 – 0 – 1, ventral 0; patella, dorsal 1 (weak) – 1, elsewhere 0; tibia, dorsal 1 – 0 – 1, prolateral 1 – 1 – 1, retrolateral 1 – 1 – 1, ventral 0 – 1 – 1; metatarsus, dorsal 1 – 0 – 0, prolateral 1 – 0 – 0, retrolateral 0 – 1 – 1 – 0, ventral 1 (weak) – 1 (weak) – 0 – 0. Second leg: femur, dorsal 0, prolateral 0 – 0 – 1, retrolateral 0 – 0 – 1, ventral 0; patella, same as in first leg; tibia, dorsal same as in first leg, prolateral 1 (weak) – 0 – 1, retrolateral 1 – 1,

ventral 0 – 0 – 1; metatarsus, dorsal 1 – 0 – 0, prolateral 1 – 1 – 0 – 0, retrolateral 0 – 1 – 0, ventral 1 (weak) – 1 (weak) – 0 – 0. Third leg: femur, dorsal 0, prolateral 0 – 0 – 1, retrolateral 0 – 0 – 1, ventral 0; patella, dorsal 1 (weak) – 1, elsewhere 0; tibia, dorsal 0, prolateral 0 – 1, retrolateral 1 – 0, ventral 0 – 1 – 0; metatarsus, dorsal 1 – 0, prolateral 1 (middle), retrolateral 0, ventral 1 – 0. Fourth leg: femur, dorsal 0, prolateral 0 – 0 – 1, retrolateral 0 – 0 – 1, ventral 0; patella, dorsal 1 (weak) – 1, prolateral 0, retrolateral 0, ventral 0; tibia, dorsal 1 – 0, prolateral 1 – 0 – 1, retrolateral 0 – 0 – 1, ventral 0. Trichobothria and claws essentially as in male.

Abdomen. — Essentially as in male (Figs. 4–5). Two pairs of dorsal tubercles, of which posterior ones are much the larger. A single tracheal spiracle just anterior to well-developed colulus. Spinnerets as in male. Anal tubercle prominent, flattened.

Color in alcohol. — Essentially as in male except that colored areas are larger and more intense. Dusky submarginal stripes on cephalothorax darker in female and extending to lateral eyes, with a break at cephalic groove and another just posterior to lateral eyes. Elongate triangular dusky spot, which occurs in most males directly in front of the thoracic pit, in female extending throughout eye region, where gray color is more or less broken into patches. Posterior half of sternum bright red, with narrow extensions of this color anteriorly along margin. Lateral sides of abdomen more or less striped with black and mottled with red around black-striped area. Ventral postgenital spot large, reddish in the middle, black-bordered. White angular areas on abdomen more prominent than those described for male by Petrunkevitch (1939). Anterior spinnerets darker than in male, otherwise the same. About half way between anal tubercle and posterior abdominal humps an irregular dark spot consisting of five or six narrow cross bands observed in both sexes, but more evident in female. White patches of guanine dorsally, within region bounded by the four humps, as in male, and small spots of black and red also. Anterior humps tipped with black in female allotype, also faintly indicated in males in my collection. Legs all prominently ringed with reddish brown. These rings, although not mentioned in description of holotype male, found to be essentially the same in the two sexes, except often indistinct in male.

Epigynum. — Simple, with a fairly prominent, somewhat hairy lobule (Figs. 6–8).

Type locality. — Female allotype from Barro Colorado Island, Canal Zone, August, 1939. Female paratypes and males from same locality, June–August, 1934, 1936, 1939.

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THE GENUS *VESPULA* (HYMENOPTERA, VESPIDAE) IN MICHIGAN, WITH KEYS AND DISTRIBUTION

ROBERT R. DREISBACH

THE genus *Vespula* is a homogeneous, easily recognized group of wasps. Dr. Joseph Bequaert's paper on the hornets and yellow jackets of America (*Entomologica Americana*, N. S., 12[1931]: 71–138) makes another set of keys almost superfluous. However, since there are twenty species and varieties in that paper, whereas here only twelve are considered, the keys become somewhat simpler and easier to use.

The writer wishes to express his indebtedness to Dr. Bequaert for his determination and checking of species, and for his suggestions and criticism; and to Mr. F. M. Gaige, of the University of Michigan Museum, and Miss Eugenie McDaniels, of Michigan State College, who made available the specimens of this genus in the collections under their charge; also to Dr. Don Irish, of Midland, Michigan, through whose kindness the photomicrographs of the male genitalia were obtained.

The genus *Vespula*, family Vespidae, is a member of the superfamily Vespoidea of the aculeate Hymenoptera. The family Vespidae may be separated from the other families of the Vespoidea on the basis of the following characteristics:

Fore wings folded longitudinally in repose; antennae with 12 joints in female, 13 in male; first discoidal cell very long, generally much longer than submedian; transverse median vein in hind wing angulate; antennae not noticeably swollen apically; second cubital cell receiving both recurrent nervures.

Some of the terms used in the keys are:

Posterior orbits, that portion of the head just behind the compound eyes and bordering them from the base of the mandibles to the vertex.

Oculomalar space, the space between the lower front margin of the compound eyes and the base of the mandibles.

Tergite, the dorsal portion of an abdominal segment.

Sternite, the ventral portion of an abdominal segment.
Clypeus, the space from just below the insertion of the antennae to the front margin and extending laterally to the compound eyes.
Aedeagus, the male intromittent organ.

KEY TO THE SUBFAMILIES OF MICHIGAN VESPIDAE

1. Mandibles more or less elongate and knifelike, crossing each other or extended forward to form a beak, their inner margins toothed or notched; middle tibiae with one spur (very rarely with two or none); clypeus broadly rounded, truncate or emarginate at tip (very rarely pointed) Eumeninae
1. Mandibles short and broad, obliquely truncate and toothed at apex, folding above one another under clypeus or slightly crossing; middle tibiae with two spurs 2

2. Clypeus broadly truncate and more or less emarginate at apex; first abdominal tergite vertically truncate anteriorly; hind wing without an anal lobe, basal third strongly narrowed. (Hornets and yellow jackets) Vespinae
2. Clypeus pointed at apex, rarely rounded or straight; first abdominal tergite not vertically truncate and never narrowed into a stalk; hind wing with an anal lobe ..... Polistinae

No attempt is made here to include the synonymy, as that has already been presented in the paper mentioned above. Eleven species and varieties of this genus have been taken in Michigan to date; since the related *Vespa crabro* L. will probably be collected in the state in the near future, it is included in the key.

KEY TO MICHIGAN VESPINAE

1. Head very large, with very wide (1.4–2.0 mm.) outer orbits; vertex long, about 1.4 mm. from posterior ocelli to posterior edge of vertex; sides of pronotum with a large vertical carina over entire upper edge ..... *Vespa crabro* L.
1. Head small, with very much narrower outer orbits; posterior ocelli very close to posterior edge of vertex; vertex approximately 0.5 mm. long; ocelli about on a line with upper edge of eyes 2

2. Oculomalar space very short, approximately 0.2 mm. long, rarely more than one fifth length of antennal scape ..... (subgenus *Vespula*) 3
2. Oculomalar space long, at least 0.5 mm., and approximately two fifths to two thirds length of antennal scape.... (subgenus *Dolichovespula*) 15

3. Two curved longitudinal yellow stripes on mesonotum, slightly shorter than mesonotum, reaching neither posterior nor anterior margin; abdomen of queen mostly orange, with anterior borders black; male and worker with abdomen mostly black, posterior margins of tergites with yellow bands ..... *Vespula squamosa* (Drury)
3. No yellow stripes on mesonotum, which is entirely black..... 4

4. Queens and workers; antennae with 12 segments 5
4. Males; antennae with 13 segments 10

5. Posterior orbits with fine ridge on their posterior edges on upper half only; erect hairs on first abdominal tergite black 6
5. Posterior orbits with fine ridge on posterior edges over whole length, down to base of mandibles; ridge may be obscured for a short distance above mandibles, but this group, at least in Michigan, has erect hairs of first abdominal tergite always yellowish, not black; antennal scape black 9

6. Pale markings whitish ..... *Vespula rufa* var. *consobrina* (Sauss)
6. Pale markings yellowish 7

7. Long erect hairs over whole length of upper side of hind tibiae; exposed part of sixth ventral abdominal segment as long as wide; third, fourth, and fifth ventral abdominal segments with large sparse punctures on posterior half, first half shining black, impunctate; no workers *Vespula austriaca* (Panzer)
7. No erect hairs over length of upper side of hind tibiae; exposed part of sixth ventral abdominal segment 1.4 broader than long in queen, slightly broader than long in workers; punctures on ventral abdominal segments smaller, surface dull, not shining 8

8. Second tergite without yellow spots; third, fourth, and fifth tergites mostly yellowish, enclosing black spots; second tergite with yellow band on posterior edge, narrow in middle and becoming broader toward sides; clypeus with three black elongate spots placed in triangle ..... *Vespula rufa* var. *vidua* (Sauss)
8. Second tergite with yellow spots; postscutellum sometimes with yellow spots also; third, fourth, and fifth tergites mostly black; clypeus with broad black band, which may be anchor-shaped *Vespula rufa* var. *acadica* (Sladen)

9. First abdominal tergite black with posterior border yellow; abdomen with much more black than in following species, especially in queens; yellow posterior border of pronotum widened outwardly; black stripe connecting antennal sockets with vertex gradually broadened above; clypeus with black band in center; yellow band on outer orbits generally interrupted by a black spot at about center *Vespula vulgaris* (L.)
9. First abdominal tergite mostly yellow, with black triangle just in front of center and with anterior lateral corners black; yellow posterior border of pronotum narrow, not widened outwardly; black stripes connecting antennal sockets with vertex much narrowed above or entirely absent; clypeus with from one to three black spots, often almost entirely yellow; yellow band on outer orbits not interrupted with black ..... *Vespula maculifrons* (R. du B.)

10. Disc of seventh abdominal tergite depressed and not evenly convex throughout; seventh abdominal sternite slightly notched at apex; aedeagus ending in an almost oval expansion 11
10. Disc of seventh abdominal tergite evenly convex throughout; seventh abdominal sternite evenly rounded and entire at apex; aedeagus shaft broad, ending in a saddle-shaped club 12

11. Disc of seventh tergite abruptly depressed at basal third; apex very faintly if at all emarginate; black spot connecting antennal sockets with vertex much narrowed above or entirely absent; first abdominal tergite with a broader yellow band on posterior edge connected with a short yellow band each side of center on anterior edge, enclosing an oblong black spot which is open in front in center
Vespula maculifrons (R. du B.), Pl. I, Fig. 1

11. Disc of seventh tergite sloping more gradually from base; apex with a very slight emargination; black stripe connecting antennal sockets with vertex gradually broadened above; first abdominal tergite with a narrow yellow band on posterior margin, anterior margin immaculate ..... *Vespula vulgaris* (L.), Pl. I, Fig. 2

12. Pale markings white .. *Vespula rufa* var. *consobrina* (Sauss . Pl. II, Fig. 1
12. Pale markings yellow 13

13. No yellow spots on second tergite; third, fourth, fifth, and sixth tergites mostly yellow, with the yellow enclosing black spots; anterior border of tergites in center, with a large V-shaped black spot; yellow band on posterior edge of pronotum broad
Vespula rufa var. *vidua* (Sauss), Pl. II, Fig. 2

13. Two yellow spots on second tergite; third, fourth, fifth, and sixth tergites mostly black, with posterior edge bordered with narrow wavy yellow bands; band on posterior edge of pronotum very narrow 14

14. Long erect hairs on upper edge of hind tibiae; a continuous yellow band on inner half of outer orbits; clypeus with narrow black band extending from center to anterior edge (yellow band on posterior orbits continuous) ..... *Vespula austriaca* (Panzer)

14. No erect hairs on upper edge of hind tibiae; yellow band on inner half of orbits interrupted in center by black spot; clypeus with a broad black band reaching from posterior to anterior edge
Vespula rufa var. *acadica* (Sladen)

15. Markings white 16
15. Markings yellow 17

16. Lower sides of pronotum finely striate; long erect hairs on head, thorax, and first abdominal tergite yellowish to white; outer orbits much broader than in following species; longitudinal ridges on under side of segments of flagellum, beginning with third segment; first three abdominal tergites entirely black, the rest margined posteriorly with broad white indented bands ..... *Vespula maculata* (L.), Pl. III, Fig. 1

16. Lower sides of pronotum smooth; long erect hairs on head, thorax, and first abdominal tergite black; no longitudinal ridges on under side of flagellum; first three abdominal tergites margined posteriorly with narrow bands of white, although band may be present only on sides of second tergite; rest of tergites margined with broader, indented, white bands; these bands narrower than in preceding species
Vespula adulterina var. *arctica* Roh., Pl. III, Fig. 2

17. Yellow posterior border of pronotum continued downward on anterior edge, along vertical carina; yellow band on posterior orbits continu-

ous, though it may be narrowed in center; yellow band on first tergite with a V-shaped notch in center; branches of aedeagus broader, not tong-shaped, at apex ..... *Vespula arenaria* (Fab.), Pl. IV, Fig. 1

17. Yellow posterior border of pronotum not continued downward along vertical carina; yellow band on posterior orbits interrupted in center with black; band on first tergite without notch; aedeagus more delicate, its branches at apex tong-shaped
Vespula norwegica var. *norvegicoides* (Sladen), Pl. IV, Fig. 2

The distributional records listed below are based on the collection in the University of Michigan, the collection of Michigan State College, the private collections of Mr. Curtis Sabrosky, Mr. George Steyskal, and the writer, and several smaller collections.

The need for further search for members of this group is shown by the fact that the species which has been found in the most localities, *Vespula arenaria* (Fab.), is known from only fifty-two counties in the state. Furthermore, no collections of *Vespula* have been made from the following twenty-one counties: Delta, Grand Traverse, Ogemaw, Mason, Muskegon, Kent, Tuscola, Ottowa, Ionia, Clinton, Shiawassee, St. Clair, Allegan, Barry, Eaton, Cass, St. Joseph, Branch, Hillsdale, Lenawee, Monroe. A great many other counties are represented by only one or two species. Cheboygan County, with eight species, has the largest number, followed by Mackinac with seven. There are four species known from Isle Royale, eight from the Upper Peninsula, and ten from the Lower Peninsula.

Vespula arenaria (Fab.), *V. maculifrons* (R. du B.), and *V. maculata* (L.) occur throughout the state and should be collected in every county. *V. adulterina* var. *arctica* Roh. has not been taken south of Clare County, but should be found in every county north of it. *V. norwegica* var. *norwegicoides* (Sladen) is a boreal species and has not been located south of Kalkaska County. Of the three varieties of *V. rufa*, var. *consobrina* (Sauss) seems to be the most northern, since it has been taken in practically all the counties of the Upper Peninsula and on Isle Royale. It is also common in the Lower Peninsula as far south as Huron County, and one collection each has been made in Livingston and Oakland counties. *V. rufa* var. *vidua* (Sauss) is not of frequent occurrence in the Upper Peninsula, but has been collected quite widely through the Lower Peninsula, and probably should be found in all the counties there. *V. rufa* var. *acadica* (Sladen) has been found only in Iosco and Kalkaska counties. *V. squamosa* (Drury) seems to reach about the

northern limit of its range in Washtenaw County, but should be present throughout the southern tier of counties.

Annotated List of Species and Varieties in Michigan

Vespula austriaca (Panzer). — According to Dr. Bequaert there are two specimens in the Museum of Comparative Zoölogy, Harvard University, labeled as from Michigan, but without the locality. One female, collected by Mr. A. W. Andrews in Chippewa County on July 10, 1913, is in the University of Michigan Museum.

Vespula maculifrons (R. du B.). — U. P.:[1] Dickinson, Alger, Chippewa. L. P.:[1] Cheboygan, Charlevoix, Leelanau, Oscoda, Alcona, Manistee, Roscommon, Lake, Clare, Gladwin, Arenac, Oceana, Mecosta, Isabella, Midland, Bay, Huron, Montcalm, Saginaw, Sanilac, Lapeer, Ingham, Livingston, Oakland, Macomb, Van Buren, Kalamazoo, Calhoun, Jackson, Washtenaw, Wayne, Berrien.

Vespula rufa var. acadica (Sladen). — Rare, the only records being from Kalkaska, collected July 8, by R. R. Dreisbach, and Iosco, collected July 16, by R. R. Dreisbach.

Vespula rufa var. consobrina (Sauss). — Isle Royale. U. P.: Keweenaw, Ontonagon, Baraga, Gogebic, Marquette, Alger, Dickinson, Schoolcraft, Luce, Chippewa, Menominee, Mackinac. L. P.: Emmett, Cheboygan, Charlevoix, Leelanau, Antrim, Benzie, Kalkaska, Crawford, Oscoda, Alcona, Midland, Bay, Huron, Livingston, Oakland.

Vespula rufa var. vidua (Sauss). — U. P.: Menominee, Mackinac. L. P.: Cheboygan, Otsego, Montmorency, Alpena, Grand Traverse, Kalkaska, Crawford, Alcona, Manistee, Wexford, Roscommon, Iosco, Lake, Osceola, Gladwin, Midland, Bay, Ingham, Livingston, Oakland, Washtenaw, Wayne.

Vespula squamosa (Drury). — Taken only twice in the state. One female was collected by Mr. Curtis Sabrosky in Van Buren County on June 23, 1938; another female, in the University of Michigan Museum, was taken on June 16, in Washtenaw County.

Vespula vulgaris (L.). — U. P.: Gogebic, Alger, Luce, Chippewa, Mackinac. L. P.: Cheboygan, Charlevoix, Kalkaska, Grand Traverse, Crawford.

[1] U. P., Upper Peninsula; L. P., Lower Peninsula.

Vespula adulterina var. arctica Roh. — U. P.: Baraga, Dickinson, Marquette, Luce, Chippewa, Menominee, Mackinac. L. P.: Cheboygan, Montmorency, Osceola, Clare.

Vespula arenaria (Fab.). — Isle Royale. U. P.: Houghton, Ontonagon, Baraga, Gogebic, Iron, Dickinson, Marquette, Alger, Schoolcraft, Chippewa, Menominee, Mackinac. L. P.: Emmett, Cheboygan, Presque Isle, Charlevoix, Leelanau, Antrim, Otsego, Montmorency, Benzie, Kalkaska, Crawford, Oscoda, Alcona, Manistee, Missaukee, Roscommon, Iosco, Lake, Osceola, Clare, Gladwin, Oceana, Newaygo, Mecosta, Isabella, Midland, Bay, Huron, Montcalm, Gratiot, Sanilac, Genesee, Lapeer, Ingham, Livingston, Oakland, Kalamazoo, Washtenaw, Wayne, Berrien.

Vespula maculata (L.). — Isle Royale. U. P.: Keweenaw, Houghton, Gogebic, Marquette, Schoolcraft, Luce, Chippewa, Mackinac. L. P.: Cheboygan, Leelanau, Otsego, Alpena, Benzie, Crawford, Oscoda, Manistee, Wexford, Missaukee, Iosco, Lake, Clare, Gladwin, Oceana, Newaygo, Isabella, Midland, Bay, Huron, Ingham, Livingston, Oakland, Kalamazoo, Washtenaw, Wayne, Berrien.

Vespula norwegica var. norvegicoides (Sladen). — Isle Royale. U. P.: Houghton, Dickinson, Mackinac. L. P.: Cheboygan, Kalkaska.

Midland, Michigan

PLATES I–IV

FIG. 1. *Vespula maculifrons* (R. du B.), male genitalia, ventral view

FIG. 2. *Vespula vulgaris* (L.), male genitalia, ventral view

FIG. 1. *Vespula rufa* var. *consobrina* (Sauss), male genitalia, ventral view

FIG. 2. *Vespula rufa* var. *vidua* (Sauss), male genitalia, ventral view

FIG. 1. *Vespula maculata* (L.), male genitalia, ventral view

FIG. 2. *Vespula adulterina* var. *arctica* Roh., male genitalia, ventral view

FIG. 1. *Vespula arenaria* (Fab.), male genitalia, ventral view

FIG. 2. *Vespula norwegica* var. *norvegicoides* (Sladen), male genitalia, ventral view

MATHEMATICAL RELATIONSHIP BETWEEN THE LENGTH AND THE AGE OF THE ROCK BASS, *AMBLOPLITES RUPESTRIS* (RAFINESQUE)

RALPH HILE

A NUMBER of species of fish, both marine and fresh-water, have been included among the animals employed for the investigation of the mathematical relationship between size and age. The equations derived have ranged in complexity from the relatively simple geometric-progression formulas developed by Ford (1933) for the marine herring and by Wagler for the northern pike (1936) and three species of coregonids (1937) to the rather complicated function applied by Pütter (1920) to the growth of Norwegian and Icelandic herrings. It does not come within the scope of this paper to undertake either a review of the various types of growth equations or a discussion of the logical and observational bases from which they were developed. Treatments of these subjects and numerous references to the literature may be found in publications by Pütter (1920), Ludwig (1929), von Bertalanffy (1934), Bückmann (1938), and others.

Directly pertinent to the subject of the present paper, however, is the growth formula derived by Weymouth and McMillin (1931) in connection with their investigation of the Pacific razor clam, *Siliqua patula*.[1] This equation, which was developed on the assumption, by no means new to biology, that the relative rate of growth decreases at a constant relative rate, took the form:

$$L = Be^{-ce^{-kt}},$$

where L = length,

t = time,

and B, c, and k = constants.

[1] Although the Weymouth and McMillin equation was not fitted to data on the growth of fish, a point in common between the methods employed for the

The curve, which is of the Gompertz type,[2] fitted the empirical data satisfactorily except in old age, when the empirical values were higher than the calculated values.

A possible objection to the equation of Weymouth and McMillin lies in the fact that it was developed from assumptions concerning the instantaneous rate of growth, although the empirical data provided information only on the length of the clams at one-year intervals. Obviously the course of growth of cold-blooded animals (with a winter slackening or cessation of growth) does not proceed along the smooth and continuous curve of the Weymouth-McMillin formula. Instead, the growth must be recognized as a periodic function whose values are defined only at unit intervals of time. Rigorous procedure would require that the assumptions from which the growth formula is developed be concerned only with size at intervals of one year and with increments of growth for one-year periods.

It is of some interest to learn what type of equation results when the basic assumption (namely, that the relative rate of growth decreases at a constant relative rate) is the same as that employed by Weymouth and McMillin, but when this relative growth is expressed only in terms of growth over finite (one-year) intervals of time.

If the relative rate of growth, $\phi(t)$, decreases at a constant relative rate we have the relationship:

$$\frac{\phi(t+1)}{\phi(t)} = B,$$

where B = a constant $(O < B < 1)$. (1)

It follows then that:

$$\phi(t) = CB^t. \quad (2)$$

C = a constant.

---

investigation of growth of certain mollusks and fish should be mentioned. Many species of both groups carry a history of past growth in the form of "winter rings" in the hard parts of the body (shells of mollusks; scales and bones of fish). A difference lies in the fact that the past growth of mollusks is measured directly on the shells, whereas the growth histories of fish are computed (by means of various formulas) from measurements of growth zones on scales or bones.

[2] See Winsor (1932) for a review of applications of the Gompertz curve to growth phenomena.

If size as a function of time is set as $f(t)$, we have by definition of the relative rate of growth:

$$\phi(t+1) = \frac{f(t+1) - f(t)}{f(t)} = CB^{t+1}. \qquad (3)$$

From this relationship is obtained the final equation:

$$f(t) = K(CB+1)(CB^2+1)(CB^3+1) \cdot \cdot \cdot (CB^t+1). \qquad (4)$$

K = a constant.

The final equation, which takes the form of a factorial, not only has an awkward appearance but presents the difficulty that the solution for $t = n$ requires the previous solution for all values of t less than n.

Considerable success was attained in fitting the equation to data on the growth of the 1923 year class of the rock bass, *Ambloplites rupestris*, of Nebish and Muskellunge lakes (Wisconsin). This year class was of such great abundance that large numbers could be taken at relatively advanced ages. Two circumstances contributed greatly to the reliability of the data as a true measure of the natural course of growth of rock bass in these lakes. The method of computing growth histories from scale measurements involved no large approximations, but was developed from a careful study of the actual relationship between body length and scale length. Furthermore, extensive data on the fluctuations (presumably from environmental causes) of growth rate in different calender years made possible the "correction" of the growth curves for the year class to eliminate distortion of the data from that source.

The data of Tables I and II on the growth of the 1923 year class of the Nebish Lake rock bass are based on 117 males and 99 females captured in 1931 during the ninth year of life and on 41 males and 74 females taken in 1932 during the tenth year of life. In the tables are presented: the average calculated lengths (second column) and increments of length (third column) as actually computed from scale measurements; the quality of growth in different years expressed as percentages of average or "normal" growth (fourth column); the calculated increments of length (fifth column) and calculated lengths (sixth column) after "correction" to eliminate the effects of annual fluctuations in growth rate; the empirical values of the relative growth rate, $\phi(t)$ (seventh column); and the values of the ratio,

TABLE I

GROWTH OF MALE NEBISH LAKE ROCK BASS OF THE 1923 YEAR CLASS

Standard lengths and annual increments of length as computed originally from scale measurements and as corrected to eliminate the effects of fluctuations in the quality of growth (given in table as percentages of average or "normal" growth) in different calendar years. At the right of the table are the empirical values of the relative growth rate, $\phi(t)$, and of $\phi(t+1)/\phi(t)$.

Year of life	Calculated length in millimeters	Increment of length	Quality of growth in calendar year of increment	"Corrected" increment	"Corrected" calculated length	$\phi(t)$	$\frac{\phi(t+1)}{\phi(t)}$
1	37.1	37.1	112.8	32.9	32.9	...	...
2	63.2	26.1	90.9	28.7	61.6	0.8723	...
3	93.2	30.0	95.6	31.4	93.0	0.5097	0.5843
4	120.2	27.0	95.1	28.4	121.4	0.3054	0.5992
5	140.0	19.8	91.9	21.5	142.9	0.1771	0.5799
6	152.6	12.6	84.8	14.9	157.8	0.1043	0.5889
7	163.7	11.1	98.1	11.3	169.1	0.0716	0.6865
8	171.8	8.1	108.4	7.5	176.5	0.0444	0.6201
9	180.0	8.2	120.6	6.8	183.4	0.0385	0.8671

$\frac{\phi(t+1)}{\phi(t)}$ (eighth column). The method of computing growth histories from scale measurements and the procedure for determining annual deviations from average growth have been described by Hile (1941).

In the data for the male rock bass, only the first four values of $\frac{\phi(t+1)}{\phi(t)}$ tended to fluctuate about a constant level; beyond the sixth year of life, therefore, the growth of the males failed to conform to the style of growth assumed for the derivation of equation (4). For this reason, only the data on growth during the first six years were employed in fitting the equation to the observed calculated lengths. The curve for the females also was fitted to the data for the first six years, although the values of $\frac{\phi(t+1)}{\phi(t)}$ in Table II prove the selection of this period to be to a certain extent arbitrary.

Table III contains comparisons of the original growth data of the 1923 year class of the Nebish Lake rock bass with lengths computed from equation (4). At the bottom of the table may be found the values of the constants B, C, and K. The equation fitted the

TABLE II

GROWTH OF FEMALE NEBISH LAKE ROCK BASS OF THE 1923 YEAR CLASS

Standard lengths and annual increments of length as computed originally from scale measurements and as corrected to eliminate the effects of fluctuations in the quality of growth (given in table as percentages of average or "normal" growth) in different calendar years. At the right of the table are the empirical values of the relative growth rate, $\phi(t)$, and of $\phi(t+1)/\phi(t)$.

Year of life	Calculated length in millimeters	Increment of length	Quality of growth in calendar year of increment	"Corrected" increment	"Corrected" calculated length	$\phi(t)$	$\frac{\phi(t+1)}{\phi(t)}$
1	36.0	36.0	112.8	31.9	31.9	...	...
2	62.6	26.6	90.9	29.3	61.2	0.9185	...
3	90.5	27.9	95.6	29.2	90.4	0.4771	0.5194
4	113.8	23.3	95.1	24.5	114.9	0.2710	0.5680
5	130.8	17.0	91.9	18.5	133.4	0.1610	0.5941
6	141.6	10.8	84.8	12.7	146.1	0.0952	0.5913
7	149.9	8.3	98.1	8.5	154.6	0.0582	0.6113
8	156.5	6.6	108.4	6.1	160.7	0.0395	0.6787
9	164.5	8.0	120.6	6.6	167.3	0.0411	1.0405

TABLE III

COMPARISON OF THE GROWTH (STANDARD LENGTH IN MILLIMETERS) OF THE 1923 YEAR CLASS OF THE NEBISH LAKE ROCK BASS AS COMPUTED FROM SCALE MEASUREMENTS AND AS CALCULATED BY MEANS OF EQUATION (4)

The values of the constants of the equation for fish of each sex are given.

Year of life	Males			Females		
	Length from scale measurements	Length from equation	Difference	Length from scale measurements	Length from equation	Difference
1	32.9	32.9	0.0	31.9	32.0	0.1
2	61.6	61.6	0.0	61.2	60.1	− 1.1
3	93.0	93.2	0.2	90.4	90.1	− 0.3
4	121.4	121.3	− 0.1	114.9	115.7	0.8
5	142.9	142.9	0.0	133.4	134.3	0.9
6	157.8	157.8	0.0	146.1	146.6	0.5
7	169.1	167.5	− 1.6	154.6	154.2	− 0.4
8	176.5	173.5	− 3.0	160.7	158.8	− 1.9
9	183.4	177.2	− 6.2	167.3	161.4	− 5.9
Values of constants	B 0.5881			B 0.5682		
	C 2.5238			C 2.7187		
	K 13.2350			K 12.5854		

TABLE IV

GROWTH OF MALE MUSKELLUNGE LAKE ROCK BASS OF THE 1923 YEAR CLASS

Standard lengths and annual increments of length as computed originally from scale measurements and as corrected to eliminate the effects of fluctuations in the quality of growth (given in table as percentages of average or "normal" growth) in different calendar years. At the right of the table are the empirical values of the relative growth rate, $\phi(t)$, and of $\phi(t+1)/\phi(t)$.

Year of life	Calculated length in millimeters	Increment of length	Quality of growth in calendar year of increment	"Corrected" increment	"Corrected" calculated length	$\phi(t)$	$\frac{\phi(t+1)}{\phi(t)}$
1	33.8	33.8	104.9	32.2	32.2	...	...
2	50.8	17.0	102.0	16.7	48.9	0.5186	...
3	66.6	15.8	98.4	16.1	65.0	0.3292	0.6348
4	85.4	18.8	85.6	22.0	87.0	0.3385	1.0283
5	103.1	17.7	83.4	21.2	108.2	0.2437	0.7199
6	118.8	15.7	86.6	18.1	126.3	0.1673	0.6865
7	138.9	20.1	106.6	18.9	145.2	0.1496	0.8942
8	154.4	15.5	97.1	16.0	161.2	0.1102	0.7366
9	167.2	12.8	100.8	12.7	173.9	0.0788	0.7151

empirical data remarkably well over the first six years. The maximum deviations of the calculated lengths from the empirical values were 0.2 millimeter for the males and 1.1 millimeters for the females. The average deviations were 0.05 millimeter for the males and 0.62 millimeter for the females. The extrapolated portion of the curve, however, tended to fall below the empirical values. (The failure of growth formulas to describe growth late in life appears to be fairly common.)

The data of Tables IV, V, and VI on the 1923 year class of the Muskellunge Lake rock bass correspond exactly to the data given in Tables I, II, and III for the Nebish Lake rock bass. The numbers of fish on which the growth curves of the 1923 year class of the Muskellunge Lake rock bass were based were: 1930 — 18 males and 27 females in the eighth year of life; 1931 — 53 males and 68 females in the ninth year of life; and 1932 — 9 males and 10 females in the tenth year of life.

Although the values of $\frac{\phi(t+1)}{\phi(t)}$ varied more widely in the Muskellunge Lake rock bass than in the Nebish Lake rock bass, these variations were without detectable trend in the data for the Muskellunge

TABLE V

GROWTH OF FEMALE MUSKELLUNGE LAKE ROCK BASS OF THE 1923 YEAR CLASS

Standard lengths and annual increments of length as computed originally from scale measurements and as corrected to eliminate the effects of fluctuations in the quality of growth (given in table as percentages of average or "normal" growth) in different calendar years. At the right of the table are the empirical values of the relative growth rate, $\phi(t)$, and of $\phi(t+1)/\phi(t)$.

Year of life	Calculated length in millimeters	Increment of length	Quality of growth in calendar year of increment	"Corrected" increment	"Corrected" calculated length	$\phi(t)$	$\frac{\phi(t+1)}{\phi(t)}$
1	33.4	33.4	104.9	31.8	31.8	...	...
2	51.0	17.6	102.0	17.3	49.1	0.5440	...
3	66.3	15.3	98.4	15.5	64.6	0.3157	0.5803
4	83.3	17.0	85.6	19.9	84.5	0.3080	0.9756
5	98.7	15.4	83.4	18.5	103.0	0.2189	0.7107
6	112.1	13.4	86.6	15.5	118.5	0.1505	0.6875
7	131.0	18.9	106.6	17.7	136.2	0.1494	0.9927
8	144.4	13.4	97.1	13.8	150.0	0.1013	0.6780
9	153.8	9.4	100.8	9.3	159.3	0.0620	0.6120

TABLE VI

COMPARISON OF THE GROWTH (STANDARD LENGTH IN MILLIMETERS) OF THE MUSKELLUNGE LAKE ROCK BASS AS COMPUTED FROM SCALE MEASUREMENTS AND AS CALCULATED FROM EQUATION (4)

The values of the constants of the equation for fish of each sex are given.

Year of life	Males			Females		
	Length from scale measurements	Length from equation	Difference	Length from scale measurements	Length from equation	Difference
1	32.2	32.0	− 0.2	31.8	31.0	− 0.8
2	48.9	48.2	− 0.7	49.1	47.4	− 1.7
3	65.0	67.0	2.0	64.6	66.0	1.4
4	87.0	87.2	0.2	84.5	85.4	0.9
5	108.2	107.5	− 0.7	103.0	104.2	1.2
6	126.3	126.9	0.6	118.5	121.4	2.9
7	145.2	144.7	− 0.5	136.2	136.4	0.2
8	161.2	160.3	− 0.9	150.0	148.9	− 1.1
9	173.9	173.7	− 0.2	159.3	159.2	− 0.1
Values of constants	B 0.7736			B 0.7481		
	C 0.8423			C 0.9399		
	K 19.3985			K 18.2219		

Lake fish. In other words, the general style of growth of rock bass from Muskellunge Lake conformed approximately to that assumed originally throughout the nine years of life covered by the data, whereas in Nebish Lake the actual growth deviated notably from the theoretical beyond the sixth year of life.

The comparison of the theoretical lengths (equation based on data for all nine years of life) of Muskellunge Lake rock bass with the empirical calculated lengths reveals a reasonably good agreement. The average of the absolute values of the deviations was 0.67 millimeter for the males and 1.14 millimeters for the females. These average deviations were considerably larger than the corresponding deviations of 0.05 millimeter and 0.62 millimeter for the males and females of the Nebish Lake rock bass (first six years of life only).

The outstanding difference between the growth of the rock bass in Nebish Lake and that in Muskellunge Lake lies in the fact that in the former lake it deviated rather consistently from the theoretical curve beyond the sixth year, whereas in the latter the agreement between the lengths computed from the growth equation and the empirical lengths computed from scale measurements was fair throughout the nine years of life covered by the data. A possible explanation of this difference is suggested by the comparison of empirical and theoretical annual increments of length of rock bass of the two stocks (Table VII). In the Nebish Lake rock bass the empirical and theoretical increments of length agreed well during the first six years of life. It is true that in the data for the females differences as great as 1.2 and 1.1 millimeters occurred (second and fourth years of life, respectively). These maximum deviations were, however, of opposite signs and therefore most probably represent random errors. Beyond the sixth year of life the situation changed, for the empirical increments were consistently greater than the theoretical increments. The differences ranged from 1.5 to 3.1 millimeters in the males and from 0.9 to 4.0 millimeters in the females. In the Muskellunge Lake rock bass the differences between the empirical and the theoretical increments of length, although at times fairly large, apparently were distributed at random, that is, were not correlated with age.

The Nebish Lake data were characterized also by the extremely low values of the theoretical increments of length in the last three years of life (from 9.7 to 3.7 millimeters for the males and from 7.6

TABLE VII

Comparison of Increments of Length (in Millimeters) of Nebish Lake and Muskellunge Lake Rock Bass as Computed from Scale Measurements and as Computed from Equation (4)

Year of life	Nebish Lake				Muskellunge Lake			
	Males		Females		Males		Females	
	Computed from scale measurements	Computed from equation	Computed from scale measurements	Computed from equation	Computed from scale measurements	Computed from equation	Computed from scale measurements	Computed from equation
1	32.9	32.9	31.9	32.0	32.2	32.0	31.8	31.0
2	28.7	28.7	29.3	28.1	16.7	16.2	17.3	16.4
3	31.4	31.6	29.2	30.0	16.1	18.8	15.5	18.6
4	28.4	28.1	24.5	25.6	22.0	20.2	19.9	19.4
5	21.5	21.6	18.5	18.6	21.2	20.3	18.5	18.8
6	14.9	14.9	12.7	12.3	18.1	19.4	15.5	17.2
7	11.3	9.7	8.5	7.6	18.9	17.8	17.7	15.0
8	7.5	6.0	6.1	4.6	16.0	15.6	13.8	12.5
9	6.8	3.7	6.6	2.6	12.7	13.4	9.3	10.3

to 2.6 millimeters for the females). In Muskellunge Lake, however, the theoretical increments for these same years of life ranged from 17.8 to 13.4 millimeters for the males and from 15.0 to 10.3 millimeters for the females. It is suggested, therefore, that the failure of the growth of the Nebish Lake rock bass to follow the theoretical course during the later years of life may be ascribed to the exceptionally small theoretical increments of length during these years. With this explanation it is held that adherence beyond the sixth year of life to the style of growth that held during the first six years would involve a depression of the metabolic rate not compatible with the continued existence of the individual. In other words, the survival of the Nebish Lake rock bass to an advanced age may have been contingent upon a departure from the "normal" course of growth.

The extremely small theoretical length increments of the Nebish Lake rock bass in the later years of life may be traced to the rapid rate of decline of the relative rate of growth. The values of B (Table III) show that among the Nebish Lake males the ratio of the relative growth rate in a particular year of life to the relative growth

rate in the preceding year was on the average 0.5881 and that the corresponding ratio for the females averaged 0.5682 (both values based on growth in the first six years of life). The corresponding ratios for the Muskellunge Lake rock bass (based on growth throughout all nine years) were 0.7736 for the males and 0.7481 for the females (Table VI). The slower rate of decrease in the relative growth rate of the Muskellunge Lake fish accounted for the larger theoretical length increments in the later (sixth to ninth) years of life and may have made possible a survival to advanced ages without departure from the "normal" style of growth. It appears, then, that the rate of decrease of the relative growth rate may be of considerable biological significance.

I wish to thank Professor C. Eisenhart, of the University of Wisconsin, who read the manuscript critically.

SUMMARY

If it is assumed that the relative growth rate, as determined from annual increments of growth in length, decreases at a constant relative rate, the relationship between length (L) and age in years (t) may be expressed by the equation $L = K(CB + 1)(CB^2 + 1)(CB^3 + 1) \cdot \cdot \cdot (CB^t + 1)$, where K, C, and B are constants. This equation described accurately the growth of the 1923 year class of the rock bass from Nebish Lake (Wisconsin) during the first six years of life, but yielded values that were too low in the sixth to ninth years of life. The equation fitted reasonably well the data on growth of the 1923 year class of the rock bass from Muskellunge Lake (Wisconsin) over the nine years of life for which data were available. It was suggested that the theoretical increments of length (computed by means of the equation) of the Nebish Lake rock bass were so small that conformity in late years with the style of growth that prevailed during the first six years might well involve a depression of the metabolic rate not compatible with the continued existence of the individual. Thus in some populations survival to an advanced age may be contingent on a departure from the "normal" style of growth.

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MASS HYBRIDIZATION BETWEEN TWO GENERA OF CYPRINID FISHES IN THE MOHAVE DESERT, CALIFORNIA

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HYBRIDIZATION in nature between fish species is being analyzed by the senior author and his associates in a series of papers of which this is one. Each of these publications emphasizes a distinct point in the biological significance of natural hybridization. The present contribution [1] stresses the high frequency of interspecific hybridization that may result when a changed environment sets the stage for extensive miscegenation. To appreciate this relation between ecology and hybridization it is necessary to picture briefly the present and past hydrography of the Mohave River Basin.

HYDROGRAPHY OF THE MOHAVE DESERT

The Mohave Desert is properly included within the Great Basin, since all its permanent waters are characterized by interior drainage. The principal stream crossing this arid waste is the Mohave River (Fig. 1). Its headwaters (Fig. 2) rise high on the northern slopes of the San Bernardino Mountains of southern California, and it follows a generally northeasterly course for more than one hundred miles across the desert to "The Sink of the Mohave" (Soda Lake, a large discharging playa just south of the town of Baker). Within the river basin there are five major regions of perennial flow, where fishes may be found: (1) the headwater region, comprising fully 90 per cent of the total water supply and lying above the point where Deep Creek (the east fork) and West Fork unite (in high water) to

[1] In this study we have been materially aided by a research grant from the Horace H. Rackham School of Graduate Studies, of the University of Michigan. Sidney Shapiro, who served well as research assistant, made a considerable proportion of the counts and measurements. As usual, Laura C. Hubbs has borne the brunt of the statistical calculations. Professor Elliot Blackwelder, of Stanford University, kindly reviewed the geological discussion.

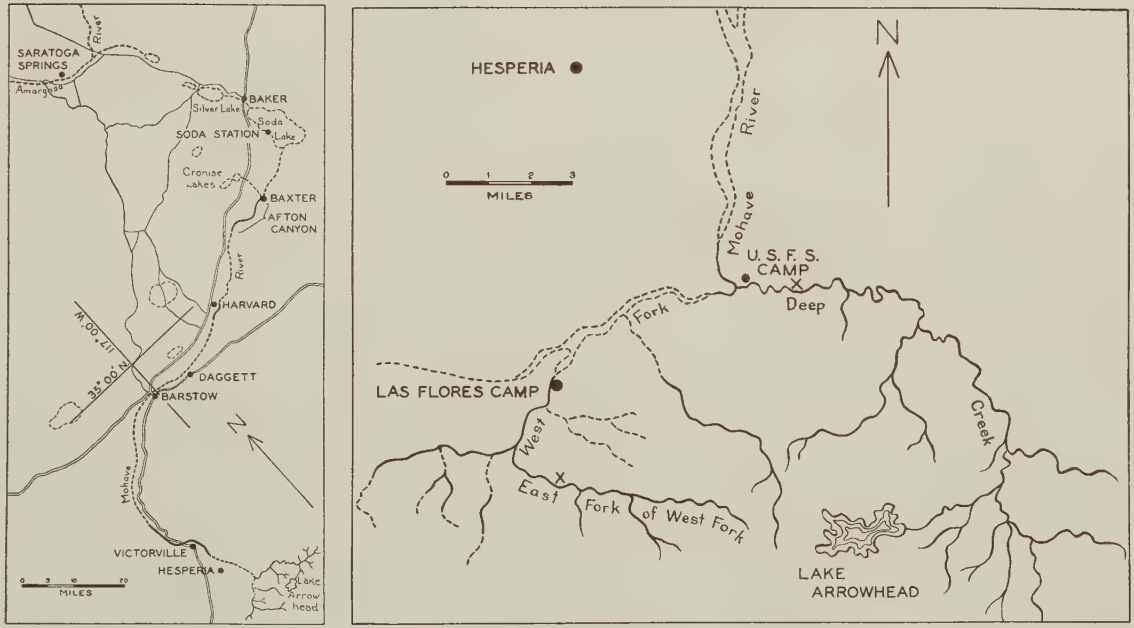

FIG. 1 (left). The present drainage features of the Mohave River system and vicinity. Perennial flows are indicated by solid lines; intermittent flows and the border of playas by dashed lines. Highways and dirt roads are also shown

FIG. 2. Detail of the headwater portion of the Mohave River system. × marks the uppermost points from which minnows have been obtained (Thomas Rodgers assisted in the drafting of both maps)

form the river proper; (2) the vicinity of Victorville, where there is a flow about seven miles in length; (3) a point south of Harvard (a railroad station about twenty miles east of Barstow), where there is a short flow; (4) Afton Canyon (about forty miles east of Barstow), where the river again flows six or seven miles; and (5) the west side of Soda Lake, at the railroad station of Soda, where a spring pool retains permanent water. Since this pond is higher than the adjacent playa bed, it is not subject to the effects of floodwaters, but all the other regions experience severe washouts from time to time.

Precipitation in the headwater region is relatively great, ranging from about 13 to 35 inches (Thompson, 1929 : 94). As a result, particularly in the Deep Creek basin, there are a considerable number of permanent and cool mountain creeks, but the stream mileage available to the native minnows is greatly restricted (Fig. 2). It is not certain to what extent the introduced trout rather than physical conditions limit the waters inhabited by minnows. As the river channel debouches from the base of the mountains onto the desert, a very rapid drop in rainfall occurs. Thus at Victorville, less than fifteen miles distant, the yearly fall is about five inches, and near Afton Canyon the precipitation is less than two inches (Thompson, 1929 : 80, 94). Consequently the occasional severe downpours in the mountainous region literally flush out the entire river (more particularly the lower portions), causing widespread change in the stream conditions and in the populations of aquatic organisms. Such a disastrous flood occurred in March, 1938, at which time the discharge not only filled Soda Lake but also overflowed into the playa of Silver Lake (the extreme flood terminus of Mohave River) just to the north. The effect of this washout on the native fishes is detailed in Table I.

The geological record clearly indicates that at some time during the Pleistocene, probably contemporaneously with lakes Lahontan and Bonneville, the waters of the Quaternary Mohave River formed a large body of water over the present playas of Silver and Soda lakes. This lake, the maximum area of which was about one hundred square miles, was named Lake Mohave by Thompson (1921 : 424). The level of its impounded waters eventually rose high enough to cut at the northern end a small outlet channel that served, for a time at least, to connect the Mohave River with the southeastern arm of Death Valley (Thompson, 1929 : 563–568). Here the stream joined the

Amargosa River, which flowed down from the north (Fig. 1). The conjoined waters contributed to the great lake (Lake Manly) which then existed in Death Valley.

Another body of water, considerably larger than Lake Mohave, is known to have covered the northeastern part of the flat valley east of Daggett. It has been called Manix Lake by Buwalda (1914 : 444). Recent studies of its deposits by Blackwelder and Ellsworth (1936) show that this lake had three stages, the first two correlated with two moist epochs during late Pleistocene time and the third possibly coincident with the close of the last ice advance. Whether it was strictly contemporaneous with Lake Mohave is not certain, but is highly probable, in the opinion of Blackwelder (personal communication).

A third Pleistocene lake, covering the present playas of East and West Cronise lakes, was formed by the Mohave River in Cronise Valley, about seventeen miles southwest of Baker (Fig. 1). Little Mohave Lake, as this body of water was named by Thompson (1921 : 424), was very much smaller than either Lake Mohave or Manix Lake, and appears to have had a very intermittent existence. Its eastern portion (East Cronise Lake) is still occasionally filled by distributary floodwaters from the Mohave River. The junior author saw minnows in that basin in 1937. According to local testimony the lake contained water from 1941 to the summer of 1942, when many fish perished as the lake dried up.

All these ancient lakes probably supported a dense population of the Mohave lake chub, *Siphateles mohavensis*, for, as is later pointed out, this species is particularly fitted for lacustrine conditions. Moreover, the record of fragmentary fish bones, identified as those of *Siphateles mohavensis*, from the first lake stage of Manix Lake (Blackwelder and Ellsworth, 1936 : 459), and another record by Buwalda (1914 : 449) of fish vertebrae (unidentified) from the same basin substantiate the presumed presence of *Siphateles* in such environments. With the disappearance of these bodies of water *Siphateles mohavensis* was largely forced to disperse into the headwater habitat of *Gila orcuttii*.

This study is one of several by which we are attempting to determine how the distribution and speciation of the fishes of the American desert have been affected by the profound hydrographic changes that occurred during and after Quaternary times (Hubbs, 1940b).

FISH FAUNA OF THE MOHAVE BASIN

With the exception of the disconnected springs and creeks of the Death Valley region, which harbor a limited fish fauna unrelated to that under consideration, as well as a few springs and short creeks that seem devoid of native fishes, all permanent waters of the Mohave Desert that have persisted into the present dry epoch are portions of the Mohave River system. These waters, now connected only in flood periods and at present probably never united into a single connected pattern, contain only two species of native fish (Pl. II). Both are members of the Cyprinidae and represent two genera that are widespread through the West. Except for brief indications by Miller (1938) and by Hubbs (1940b : 62), only one of the species, *Siphateles mohavensis* Snyder (1918), has been recorded from the basin. The second minnow seems to be inseparable specifically from *Gila*[2] *orcuttii* (Eigenmann and Eigenmann), which has hitherto been regarded as confined to the coastal streams of southern California. There are several hints that some catostomid fish occurred in the Mohave system until recently, but if it did, our extensive collecting from 1934 to 1940 indicates that it has been extirpated there.

Trout (*Salmo gairdnerii irideus*), introduced into the mountain headwaters, have probably restricted the numbers and range of the minnows. The several other exotic fishes recently added to the Mohave fauna have probably had as yet little effect on the native fish life.

Gila orcuttii and *Siphateles mohavensis* occur together, with hybrids, in nearly all parts of the generally disrupted Mohave River system (Fig. 1). The only place where the *Siphateles* appears to occur alone is in the spring pool on the ancient shore line of Quaternary Lake Mohave, of which the present southern remnant (Soda Lake) is the sump of the Mohave River. Regularly the *Gila* appears to ascend the streams farther than the *Siphateles* commonly goes, and shows more preference for the current. In the flowing streams the *Siphateles* tends to select the quieter pools.

That the *Gila* is better adapted than the *Siphateles* to stream life was dramatically proved in March, 1938, when a great flood raged

[2] The reference of this species to the genus *Gila* follows from the discovery that representatives of the nominal genera *Tigoma* and *Gila* merely represent ecological subspecies (Hubbs, 1940a : 200; 1941b : 186–187).

down the mountain sides and transformed the dry sands of the Mohave River bed into a torrent that filled the normal sump basin of Soda Lake and overflowed into the usually dry playa known as Silver Lake (Fig. 1). The force of the flood was so great that the stream beds were profoundly altered; for example, the lower end of the normal flow of Deep Creek was transformed from a large and beautiful pool (Pl. I, Fig. 4), five feet deep, into a sand-choked channel. The *Siphateles* population was swept out upon the desert in far greater proportion than was the stock of *Gila orcuttii*. As a result, the relative numbers of the two species were greatly altered. Comparing the samples of 1934 and 1937 with those taken in 1939 and 1940, we have estimated that the *Gila* population showed a relative increase of 66, 365, and 1,437 per cent in three portions of the stream system where the *Siphateles* stock decreased 89 to 93 per cent (Table I). *Siphateles* is estimated (p. 353) to have constituted 35 per cent of the Mohave minnow population in 1934 and 1937, but only 14 per cent of the total after the flood (from May, 1938, to August, 1940). That *Siphateles* was carried farther than *Gila* by the flood is indicated later (p. 355).

Siphateles mohavensis is obviously maladjusted to its present environment. Its survival may be accredited to lack of competition. There are only the two native fishes, and they are presumably complementary to a large degree in their food habits and other ecological relations.

These data on population ecology confirm the morphological evidence that had led us to regard *Gila orcuttii* as a fluviatile fish and *Siphateles mohavensis* as a lacustrine type. The *Gila* is the more streamlined: it has more turgid contours, is more terete (less slab-sided), and has a slenderer caudal peduncle (Pl. II). The *Gila* is darker and more mottled, like bottom-dwelling fishes in general; the *Siphateles* has a more uniform and more metallic color, approaching the appearance of pelagic fishes (see color descriptions, p. 372). The *Gila* has a more leathery integument and less fragile fin rays. The strong pharyngeal teeth of *Gila orcuttii* are adapted by their strong hooks and narrow grinding surfaces to a rapacious diet, presumably of stream insects; the weaker teeth of *Siphateles mohavensis*, with slight hooks and broad grinding surfaces (Pl. III), are fitted for the grinding of plankton, which is essentially a lake rather than a creek product. Correspondingly, the pharyngeal

TABLE I

RELATIVE NUMBERS OF *GILA ORCUTTII*, HYBRIDS, AND *SIPHATELES MOHAVENSIS* BEFORE AND AFTER THE GREAT FLOOD OF 1938

General locality and years	Numbers			Percentages		
	Gila	Hybrids	*Siphateles*	*Gila*	Hybrids	*Siphateles*
West Fork, Mohave River						
1934, 1937 (A) ...	22	16	78	19.0	13.8	67.2
1939, 1940 (B) ...	1,401	82	102	88.4	5.2	6.4
Change in percentage (B—A) ...	...	...	...	69.4	− 8.6	− 60.8
Hybrid index	...	...	...	...	60	...
Deep Creek						
1934, 1937 (A) ...	862	135	518	56.9	8.9	34.2
1939, 1940 (B) ...	317	10	8	94.6	3.0	2.4
Change in percentage (B—A) ...	...	...	...	37.7	− 5.9	− 31.8
Hybrid index	...	...	...	...	63	...
Mohave River near Victorville						
(1915)	...	...	(121)	...	...	(100.0)
1934, 1937 (A) ...	2	...	35	5.4	...	94.6
1939, 1940 (B) ...	332	28	40	83.0	7.0	10.0
Change in percentage (B—A) ...	...	...	...	77.6	?	− 84.6
Hybrid index	...	...	...	...	?	...

arches are stronger in *Gila* than in *Siphateles*. The long gill slits (Table XI) and numerous gillrakers (Table V) of the *Siphateles*, contrasting strongly with the similar characters of the *Gila*, are still more obvious adaptations to a plankton diet (Pl. IV). The characters of *Gila orcuttii* fit it for stream life; those of *Siphateles mohavensis* are adaptations to a lacustrine existence.

FREQUENCY OF HYBRIDIZATION

The interspecific hybridization discussed in this paper [3] was one of the two main cases that resulted in the following generalization (Hubbs, 1940b : 67): "Desiccation of waters has led to fusion as well as differentiation. Species which by their habits and by their feeding

[3] The hybridization between *Gila* and *Siphateles* was first mentioned by Miller (1938) and by Hubbs (1940b : 62).

TABLE II

RELATIVE NUMBERS OF *GILA ORCUTTII*, HYBRIDS, AND *SIPHATELES MOHAVENSIS* IN ALL AVAILABLE COLLECTIONS FROM THE MOHAVE RIVER BASIN

Locality (from headwaters to sump of Mohave River)	Numbers			Percentages		
	Gila	HYBRIDS	*Siphateles*	*Gila*	HYBRID	*Siphateles*
East Fork of West Fork of Mohave River, April 5, 1939	30	1	...	96.8	3.4	...
Same locality, Aug. 13, 1940	210	12	17	87.9	5.0	7.1
West Fork of Mohave River, Las Flores, June 29, 1937	5	4	20	17.2	13.8	69.0
Same locality, April 5, 1939	89	43	69	44.3	21.4	34.3
Same locality, July 11, 1940	176	19	12	85.0	9.2	5.8
Tributary to West Fork, Elliot Ranch, June 28, 1937	3	...	1	75(?)	...	25(?)
West Fork, Summit Valley, Aug. 31, 1934	7	4	45	12.5	7.1	80.4
Same locality, June 29, 1937	7	8	12	25.9	29.6	44.4
Same locality, July 12, 1940	518	2	3	99.0	0.4	0.6
West Fork just above Deep Creek, July 11, 1940	378	5	1	98.4	1.3	0.3
Deep Creek, about 1 mile above U. S. F. S. Camp, Sept. 27, 1931 *	...	1	2	...	33(?)	67(?)
Deep Creek at U. S. F. S. Camp, Sept. 1, 1934 (Pl. I, Fig. 4)	839	121	511	57.0	8.2	34.7
Same locality, June 30, 1937 *	23	14	7	52.3	31.8	15.9
Same locality, July 12, 1940	317	10	8	94.6	3.0	2.4
Mohave River about one fourth mile below Deep Creek, July 2, 1937	137	6	14	87.3	3.8	8.9
Mohave River about 5 miles below Deep Creek, April 5, 1939	17	...	...	100	...	...

* Sample taken with hook and line.

TABLE II (*Concluded*)

(Locality from headwaters to sump of Mohave River)	Numbers			Percentages		
	Gila	Hybrids	*Siphateles*	*Gila*	Hybrids	*Siphateles*
Floodwater pond, Mohave River, near Thorn, July 11, 1940	6	...	...	100	...	...
Spring tributary of Mohave River, near Victorville, Aug. 5, 1940	129	10	17	82.7	6.4	10.9
Mohave River, Victorville, Aug. 14, 1915	...	...	121	...	...	100
Same locality, Sept. 1, 1934	2	...	35	5.4	...	94.6
Same locality, April 8, 1939	91	18	22	69.5	13.7	16.8
Same locality, July 11, 1940	112	...	1	99.1	...	0.9
Mohave River, Daggett, March, April, May, 1903	...	...	9	...	...	100
Mohave River (stream), Afton Canyon, April 6, 1939	7	12	67	8.1	14.0	77.9
Same locality, July 26, 1940	212	63	65	62.4	18.5	19.1
Ponds in river, Afton Canyon, May 22, 1938	2	9	...	18.2	81.8	...
Same locality, April 7, 1939	6	37	122	3.6	22.4	74.0
Same locality, July 26, 1940	11	33	10	20.4	61.1	18.5
Isolated pond, Afton Canyon, April 6, 1939	16	10	13	41.0	25.6	33.3
Soda Lake spring, 1937–1940	...	...	608	...	...	100
Where species occur together (Soda Lake spring excepted)	3,350	442	1,204	67.2	8.9	24.0
1934 and 1937 (before 1938 flood)	1,023	157	645	56.1	8.6	35.3
1938 (after flood) – 1940	2,327	284	427	76.6	9.3	14.1
Grand total	3,350	442	1,812	59.9	7.9	32.2

apparatus and other structures are adapted respectively to lake life and to stream life, and which in periods of ample water no doubt had a complementary distribution, have hybridized *very extensively*

now that the two types have been forced into intimate contact in the isolated trickles and springs which represent the remnants of once expansive water systems."

The other case, that of the fluviatile *Siphateles obesus obesus* and the lacustrine *Siphateles obesus pectinifer*, of the Lahontan system, is almost exactly parallel in genetic as well as in historical and ecological respects. Almost the same difference in number of gillrakers is involved. It is somewhat arbitrary that we regard the second case as one of subspecific intergradation rather than one of interspecific hybridization. Failing to recognize the numerous intermediates that occur where the two kinds meet, Snyder (1917: 60–67, figs. 4–6) treated *Siphateles obesus* and *Leucidius pectinifer* as even generically distinct. Furthermore, he described (pp. 58–59), on the basis of only four specimens from Lake Tahoe, a new species, *Richardsonius microdon*, which is obviously a hybrid between *Richardsonius egregius* and *Siphateles obesus*. This hybrid has many features in common with the one we are describing — particularly the intermediate character of dentition, gillrakers, and scales.

An abundance of material, taken in 1934 and 1937 (before the deluge of March, 1938), as well as after the flood, in 1938, 1939, and 1940, makes it possible for us to estimate the relative numbers of the parent species and the hybrids (Table II) in the Mohave basin. From the entire stream system we have random samples totaling 5,604 cyprinids,[4] of which the percentage composition is approximately:

Gila, 60; hybrids, 8; *Siphateles*, 32.

Exclusive of the *Siphateles* samples (608 specimens) from the Soda Lake spring, where this genus alone occurs, the percentages are about:

Gila, 67; hybrids, 9; *Siphateles*, 24.

The most significant single collection was that made in the lowest pool on Deep Creek (p. 348; Pl. I, Fig. 4), where the entire popula-

[4] Most of the material studied is in the fish collection of the University of Michigan Museum of Zoology. One collection in the Natural History Museum of Stanford University and one at Field Museum have also been studied, with the kind permission of the authorities of these institutions. The available collections, taken over several years, we judge to constitute between 1 and 10 per cent of the total standing population in the entire river system, at times when the surface waters are at a very low stage.

tion of 1,471 minnows was preserved on September 1, 1934. Here the percentages are as follows:

Gila, 57; hybrids, 8; *Siphateles*, 35.

The hybrid ratio for the whole basin was scarcely affected by the great flood of March, 1938:

Data for 1934 and 1937: *Gila*, 56.1 %; hybrids, 8.6 %; *Siphateles*, 35.3 %.
Data for 1938 (May) to 1940: *Gila*, 76.6 %; hybrids, 9.3 %; *Siphateles*, 14.1 %.

The flood of March, 1938, did cause some local changes in the hybrid ratio. The percentage of the hybrids in the population decreased in the headwater streams after 1938 (Table I). This loss was compensated for by the extremely high percentage of hybrids in the river and ponds in Afton Canyon from May, 1938, to August, 1940: [5]

Gila, 254 (37 per cent)
Hybrids, 164 (24 per cent)
Siphateles, 277 (40 per cent)

An average hybrid ratio of 8 or 9 per cent of the total population, increasing locally to at least 24 per cent, is indeed very exceptional, even in the Cyprinidae. Such a transgression of specific (and generic) lines involves a severe breakdown in the isolating mechanism. It would be expected, from observations as well as from theoretical considerations, that because of its biotic inefficiency such extensive hybridization between species would ordinarily be selected against. Interspecific hybrids are ordinarily infertile, in at least one sex, yet they compete for food and often for spawning sites. Some crosses endowed with hybrid vigor more than hold their own in such competition (as do the sunfishes — Hubbs and Hubbs, 1931–33).

Such a frequency of interspecific hybridization is rarely encountered, except where certain species, as *Salmo clarkii* and *Salmo gairdnerii*, are mixed by introductions. There is a possibility that the present case of hybridization is due to the introduction of *Gila orcuttii* from southern California, as a bait minnow, into the realm of *Siphateles mohavensis*. Only *Siphateles* is represented in the Mo-

[5] This canyon contained fish in 1936 (Miller, 1936), but neither pools nor fish in 1937 (Miller, 1938). The identification of the fish occurring in Afton Canyon in 1936 is uncertain, though the published tooth counts suggest that some hybrids as well as *Siphateles* were present.

have River collections of 1903 and 1915 — the only available series that were taken prior to 1931 (Table II). Slight differences between the specimens from the desert and those from the coastal streams, however, suggest that *Gila* is native to the Mohave River system.

We interpret the mass hybridization between *Gila orcuttii* and *Siphateles mohavensis* as having been made possible by reason of the very limited competition that exists between these species. They appear to be the only native fishes of the Mohave basin, and they are to a large degree complementary in their ecology (p. 347). In these desert waters the physical rather than the biotic environment seems to be the dominant factor in the struggle for existence.

EVIDENCE FOR HYBRID INTERPRETATION

The evidence that *Gila orcuttii* and *Siphateles mohavensis* hybridize in the Mohave River system is circumstantial rather than experimental, but nevertheless trustworthy, in our opinion. This type of evidence for natural hybridization has been discussed and, we think, validated in recent papers (Hubbs and Kuronuma, 1942; Hubbs, Hubbs, and Johnson, *in press*; Hubbs, Walker, and Johnson, *in press*). In these publications there is a detailed consideration of the character index, the hybrid index, and other analytical methods now being used in the interpretation of natural hybrids. In the present study the percentage *hybrid index* is computed on the basis of fixing the average values of the characters of the more primitive parental form, *Gila orcuttii*, as 0, and the values for *Siphateles mohavensis* as 100.

The theory that *Gila orcuttii* and *Siphateles mohavensis* hybridize extensively throughout most of the Mohave River system is thoroughly in line with the ecological picture. As noted on page 351, these species were probably complementary in habitat during the Pluvial period, but are now forced into cohabitation. The spring at Soda Lake is the only place in the whole system where the two species have not been taken together (Table II). They probably segregate to some degree ecologically, but they very commonly swim together.

The main reason for considering certain of the Mohave minnows hybrids is the intermediacy that they display in many respects. The *Gila* × *Siphateles* show an intermediate physiological characteristic, namely, the ability to withstand great floods. We have already pointed out that the populations of the stream type *Gila orcuttii* were proportionately much less decimated by the great flood of March,

1938, than were the headwater stocks of the lacustrine type *Siphateles mohavensis*. The changes in the relative numbers of the parental species and the hybrids in the two headwater branches of the Mohave River, namely, West Fork and Deep Creek, demonstrate clearly the intermediate capacity of the hybrids to resist the scouring wash (Table I). The hybrid indexes for the difference in the relative numbers of hybrids in the two headwaters before and after the flood are respectively 60 and 63 (an indication of a slightly greater resemblance to the *Siphateles* than to the *Gila*).

The extent to which the parental species and the hybrids were washed out on the desert by the 1938 flood also indicates the intermediacy of the hybrids. The *Gila* population was enormously increased in the upper portion of the Mohave River, from the junction of West Fork and Deep Creek, near the base of the mountains, out to the region of Victorville (Fig. 1; Tables I–II). As a rule, the hybrids were washed farther, for the hybrid ratio rose to 24 per cent of the total population in Afton Canyon (p. 353 and Table II). *Siphateles* was presumably largely carried still farther, out to the playa lakes (Soda and Silver). When these lakes dried up the fish doubtless perished in large numbers, as they did after the major flood of 1916, when they formed windrows of mummies (Thompson, 1929 : 566).

In the generic characters of pharyngeal teeth and gillrakers the hybrids display not only intermediacy, but also a degree of variability that would not be expected in a fixed species. Furthermore, their characteristics do not reasonably fit into the systematic pattern that is rather consistently displayed by Western fishes.

The pharyngeal-tooth formula of *Gila orcuttii* is almost consistently 2, 5—4, 2; that of *Siphateles mohavensis*, typically 0, 5—5, 0, and commonly 0, 5—4, 0; that of the hybrids, most commonly 1, 5—4, 1 (Table III; Pl. III). In forty counts of each unit only two rare variant formulae appear in the *Gila*, and only the one variation in the *Siphateles*, whereas eight variant formulae are displayed by 62.5 per cent of the hybrids counted. The number of teeth developed by the hybrids on the several rows is intermediate (Table IV). This is particularly true of the teeth in the outer (lesser) row: *Gila* almost always has 2 strong teeth in this row, on each arch: *Siphateles* has none; the hybrids have 0 to 2 (typically 1), usually weak teeth. This is contrary to the expected pattern, for the Western species of

TABLE III

FREQUENCIES OF PHARYNGEAL-TOOTH FORMULAE IN *GILA*, HYBRIDS, AND *SIPHATELES*

The frequencies of teeth in each series are given in Table IV; forty specimens of each kind were counted.

Kind	Formula*	Frequency
Gila orcuttii	2, 5—4, 2	36
	2, 5—4, 1	2
	2, 5—5, 2	2
HYBRIDS	1, 5—4, 1	15
	0, 5—4, 0	6
	1, 5—5, 1	5
	1, 5—4, 0	5
	1, 5—4, 2	3
	0, 5—4, 1	2
	0, 5—5, 0	2
	1, 5—5, 0	1
	2, 4—5, 2	1
Siphateles mohavensis	0, 5—5, 0	30
	0, 5—4, 0	10

* Frequently individual teeth are lost, and in the older fish often are not replaced. Almost always the loss can be accounted for by the presence of alveoli and by the spacing. Missing teeth were counted, of course. In a few hybrids and in one or two of the *Gila* specimens one tooth of the outer row may have been falsely enumerated, on the basis of what appeared to be a nearly filled-in alveolus.

Cyprinidae normally have either 0 or 2 teeth in this row. The presence of a single weak tooth in the outer row may be taken as a sign of hybridization — as it is for "*Richardsonius microdon*" (p. 352).

Hybridity is also indicated by other characters of the pharyngeal teeth and by the form of the arch (Pl. III). In *Gila orcuttii* the teeth, notably the lowermost one of the main row, are wider toward the base than those of *Siphateles mohavensis;* they are strongly instead of slightly hooked; they have narrow and weak, rather than broad and conspicuous, grinding surfaces. In the *Gila* the two limbs of the arch (as measured above the uppermost tooth and below the lowermost one) are subequal; in *Siphateles* the lower limb is definitely the longer. The lower limb near the teeth is narrow and rounded in the *Gila* (particularly in the adults), but is broad and flat in the Mohave *Siphateles.* The outer face of the arch bears a shelf for the insertion

TABLE IV

FREQUENCIES OF PHARYNGEAL-TOOTH COUNTS IN *GILA*, HYBRIDS, AND *SIPHATELES*

The formulae are given in Table III.

	Tooth counts								No.	Av.	Hybrid index
	0	1	2	3	4	5	9	10			
INNER (MAIN) ROW											
Left side											
Gila orcuttii	..	..	..	..	..	40	..	..	40	5.00	..
HYBRIDS	..	..	..	..	1	39	..	..	40	4.98	..
Siphateles mohavensis	..	..	..	..	..	40	..	..	40	5.00	..
Right side											
Gila orcuttii	..	..	..	..	38	2	..	..	40	4.05	..
HYBRIDS	..	..	..	..	31	9	..	..	40	4.23	33
Siphateles mohavensis	..	..	..	..	10	30	..	..	40	4.75	..
Both sides (sum)											
Gila orcuttii	..	..	..	..	..	..	38	2	40	9.05	..
HYBRIDS	..	..	..	..	..	..	32	8	40	9.20	21
Siphateles mohavensis	..	..	..	..	..	..	10	30	40	9.75	..
OUTER (LESSER) ROW											
Left side											
Gila orcuttii	..	..	40	..	..	..	..	..	40	2.00	..
HYBRIDS	10	29	1	..	..	..	..	..	40	0.77	61
Siphateles mohavensis	40	..	..	..	..	..	..	..	40	0.00	..
Right side											
Gila orcuttii	..	2	38	..	..	..	..	..	40	1.95	..
HYBRIDS	14	22	4	..	..	..	..	..	40	0.75	62
Siphateles mohavensis	40	..	..	..	..	..	..	..	40	0.00	..
Both sides (sum)											
Gila orcuttii	..	..	..	2	38	..	..	..	40	3.95	..
HYBRIDS	8	8	20	3	1	..	..	..	40	1.53	61
Siphateles mohavensis	40	..	..	..	..	..	..	..	40	0.00	..

of the two outer teeth in *Gila*, but in *Siphateles* has an even and steep slope, so that teeth could hardly find a base if they ever were present. In all these features of teeth and arch the hybrids are intermediate; or, commonly, they show a mixture of the features of the parental types. It seems that dental maladjustments occur in fish hybrids as well as in heterogeneous crosses in man and in dogs (Stockard and Johnson, 1941 : 367–383).

Similarly impressive variable intermediacy is exhibited by the characters of the gill arches (Pl. IV). In harmony with its presum-

TABLE V

FREQUENCIES OF GILLRAKER COUNTS IN *GILA ORCUTTII*, HYBRIDS, AND *SIPHATELES MOHAVENSIS*

Locality (see next page)	Kind	Number of gillrakers																						
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
A	*Gila*	..	9	22	10	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	HYBRIDS	..	..	...	...	2	3	10	13	5	1	2	2	..	..	..	..	..	..	..	..	..	..	..	..
	Siphateles	..	..	...	...	..	..	..	..	..	..	..	..	..	3	3	6	7	11	10	9	3	3	2	..
B	*Gila*	5	16	63	27	12	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	HYBRIDS	..	..	...	...	2	3	16	32	41	16	2	2	..	..	..	..	..	..	..	..	..	..	..	..
	Siphateles	..	..	...	...	..	..	..	..	..	..	..	..	2	2	2	1	5	20	21	25	20	8	4	..
C	*Gila*	5	28	77	39	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	HYBRIDS	..	..	...	...	..	1	3	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Siphateles	..	..	...	...	..	..	..	..	..	..	..	..	..	2	..	..	..	3	3	2	2	1	1	..
D	*Gila*	1	15	19	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	HYBRIDS	..	..	...	...	..	..	3	11	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	Siphateles	..	..	...	...	..	..	..	..	..	..	..	..	..	..	..	2	2	3	7	4	2	1	..	1
E	*Gila*	2	9	38	21	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	HYBRIDS	..	..	2*	1*	11	11	7	15	7	2	4	5	1	..	..	..	..	..	..	..	..	..	..	..
	Siphateles	..	..	...	...	..	..	..	..	..	..	..	..	..	..	1	3	8	10	21	13	7	3	..	..
F	*Siphateles*	..	..	...	...	..	..	..	..	..	..	..	..	..	..	1	4	6	17	19	20	9	2	2	..
A–F	*Gila*	13	77	219	102	20	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	HYBRIDS	..	..	2*	1*	15	18	39	71	56	22	8	9	1	..	..	..	..	..	..	..	..	..	..	..
	Siphateles	..	..	...	...	..	..	..	..	..	..	..	..	2	7	7	16	28	64	81	73	43	18	9	1

* Each count of 8 or 9 on one side of a hybrid is matched by a count of 11 on the other side; only a few specimens were counted on both sides.

TABLE V (*Concluded*)

STATISTICAL COMPUTATIONS

Locality	Kind	Range	No.	M ± σ_M	Coefficient of variability (%)	Hybrid index
(A) West Fork of Mohave River	*Gila*	7–10	43	8.12 ± 0.15	9.65	..
	HYBRIDS	10–17	38	12.97 ± 0.26	12.44	32
	Siphateles	19–28	57	23.33 ± 0.28	9.13	..
(B) Deep Creek	*Gila*	6–10	123	8.20 ± 0.08	10.20	..
	HYBRIDS	10–17	114	13.52 ± 0.11	9.04	33
	Siphateles	18–28	110	24.38 ± 0.18	7.90	..
(C) Mohave River, ¼ to 5 miles below Deep Creek	*Gila*	6–10	154	8.07 ± 0.07	10.29	..
	HYBRIDS	11–15	6	12.67 ± 0.61	10.85	29
	Siphateles	19–28	14	24.00 ± 0.67	10.45	..
(D) Mohave River, Victorville	*Gila*	6–9	40	7.70 ± 0.11	9.28	..
	HYBRIDS	12–15	18	13.17 ± 0.20	6.33	33
	Siphateles	21–29	22	24.14 ± 0.39	7.63	..
(E) Mohave River, Afton Canyon	*Gila*	6–10	71	8.14 ± 0.09	9.29	..
	HYBRIDS	8–18	66	12.58 ± 0.29	18.57	28
	Siphateles	20–27	66	23.95 ± 0.19	6.35	..
(F) Soda Lake spring	*Siphateles*	20–28	80	24.09 ± 0.18	6.54	..
(A–F) All localities	*Gila*	6–10	431	8.09 ± 0.04	10.44	..
	HYBRIDS	8–18	242	13.13 ± 0.11	12.87	32
	Siphateles	18–29	349	24.03 ± 0.10	7.89	..

ably entomophagous habits, *Gila orcuttii* has the short gill slit and the few almost rudimentary gillrakers that are typical of the genus. In correlation with a probable plankton diet *Siphateles mohavensis* has deeply cleft gill slits and numerous slender functional gillrakers. In the hybrids the first gill slit is of almost exactly intermediate length (Table XI, second item); the values for the hybrid fill the gap between those for the parental species. The gillrakers number 6 to 10 in the *Gila*, 18 to 29 in the *Siphateles* (Table V). The values for the hybrids again fill the gap. Consistently through the river system the gillrakers average about 8 in the *Gila*, 13 in the hybrids, and 24 in the *Siphateles*. Only 19 of the 242 counts for the hybrids overlap the range of counts for both parental types. The coefficient of variability is about 10 per cent for the *Gila* and 8 per cent for the *Siphateles*, but definitely higher, 13 per cent, for the hybrids. A variation of 11 in the gillraker counts that average only 13 would be quite unexpected in any single form of fish that does not vary geographically in this respect. No explanation other than hybridization would be plausible.

Similar intermediacy is displayed by the scale structure (Pl. I, Figs. 1–3), which is strikingly different in *Gila orcuttii* and *Siphateles mohavensis*. The lateral scales of the *Gila* are typically much longer than high, have straightish upper and lower edges, and do not appear shield-shaped. Those of the *Siphateles* have more nearly equal axes and are strongly shield-shaped. The *Gila* scales have more radii, which extend onto the lateral (dorsal and ventral) fields and often occur on the basal field. The radii of the *Siphateles* are fewer, generally stronger, and more regular, and do not extend onto the lateral fields. In all these respects the hybrids cry out their intermediacy. Counts of radii for twenty adults of each form are given in Table VI.

The difference in the number of scales is not great, but the averages for all twelve enumerations (Table VII) are higher in the *Gila* than in the *Siphateles*. The averages for the hybrids are in general nicely intermediate, but with notable exceptions. The transverse counts tend to be high, and that from the origin of the dorsal fin to the lateral line is even higher than that in the *Gila*, giving a strange hybrid index of − 24. This aberrancy in the scale count is quite in agreement, however, with the fact that the measurement of the line along which this count was made, from the origin of the dorsal fin to the lateral line, averages definitely higher in the

TABLE VI

FREQUENCIES OF COUNTS OF SCALE RADII IN *GILA*, HYBRIDS, AND *SIPHATELES*

Based on adults used in Table XIII. Only those radii reaching the scale margin were counted. The scale selected was the one in the row next above the lateral line, directly over the insertion of the pelvic fin.

Kind	Number of scale radii									No.	Range	Av.	Hybrid index
	6–8	9–11	12–14	15–17	18–20	21–23	24–26	27–29	30–32				
Gila orcuttii ..	..	..	4	3	4	5	..	2	2	20	12–32	20.30	..
HYBRIDS	..	10	5	2	3	..	..	..	..	20	10–19	12.60	61
Siphateles mohavensis .	14	5	1	..	..	..	..	..	..	20	6–12	7.75	..

hybrids than in either parental species (Table XIII). This proportionately greater depth of the hybrids above the lateral line may well become established at the stage when the scales are formed there. It is a principle of lepidogenesis that more scales are laid down where there is greater space (Hubbs, 1941a).

The hybrids are interjacent in the number of fin rays, again with one significant exception. The sharpest differences lie in the number of pelvic rays, which typically number 8 in the *Gila*, 9 in the hybrids, and 10 in the *Siphateles* (Table VIII, first item). In the two large series counted the hybrid indices are 63 and 73, which indicates a somewhat greater similarity to the *Siphateles* than to the *Gila*.

Intermediacy, again with a somewhat greater approach toward the *Siphateles* parent, is shown by the hybrids in the number of anal rays (Table IX). The *Gila* typically has 7 anals; the *Siphateles*, 8. The hybrids usually have 8 rays in this fin, but 7 rays occur more frequently than in the *Siphateles*. The hybrid index of course is high, averaging 78. Correspondingly, the proportionate length of the anal base is about as great in the hybrids as in the *Siphateles* (Table XIII).

The dorsal rays show a slight but probably significant difference in average number in the parental species, with a hybrid index of 23 (Table X). The difference between the averages for the hybrids and those for the *Siphateles* is probably significant; but the averages for the hybrids and the *Gila* are not reliably different.

TABLE VII

SCALE COUNTS OF *GILA*, HYBRIDS, AND *SIPHATELES*

Based on twenty specimens of each category, all collected in lowest pool of Deep Creek, Mohave Desert, California, September 1, 1934.

Location of count	*Gila orcuttii*	HYBRIDS	*Siphateles mohavensis*	Hybrid index
Lateral line	52–63 (57.25)	49–58 (53.45)	44–55 (51.10)	62
Dorsal to lateral line	12–14 (13.20)	12–15 (13.55)	11–12 (11.75)	− 24
Anal to lateral line	8–10 (8.85)	8–9 (8.60)	7–9 (7.70)	22
Pelvic to lateral line	7–9 (7.90)	7–8 (7.55)	5–8 (6.90)	35
Predorsal scales	29–38 (34.15)	28–32 (30.20)	25–34 (28.25)	67
Predorsal rows	29–36 (32.75)	26–31 (28.60)	24–28 (26.35)	65
Around body				
above	26–29 (27.85)	25–29 (27.40)	23–27 (24.95)	16
below	23–27 (24.90)	22–27 (23.90)	20–24 (22.70)	45
total	53–58 (54.80)	49–58 (53.30)	45–52 (49.65)	29
Around peduncle				
above	14–16 (14.80)	13–16 (14.55)	12–15 (13.45)	19
below	13–15 (13.65)	12–15 (13.10)	11–14 (12.65)	55
total	29–33 (30.45)	28–32 (29.65)	25–31 (28.10)	34
			Average hybrid index	35

In the average number of pectoral rays (Table VIII) the hybrids exceed either parental species. The differences are small but almost certainly significant. The *t* values (ratios of the differences between the means to the standard error of the differences) are as follows:

Deep Creek collection:

Difference between hybrids and *Gila*, 1.29; standard error of this difference, 0.06; *t* value, 21.

Difference between hybrids and *Siphateles*, 0.36; standard error of this difference, 0.06; *t* value, 6.

Afton Canyon collection:

Difference between hybrids and *Gila*, 0.90; standard error of this difference, 0.9; *t* value, 10.

Difference between hybrids and *Siphateles*, 0.50; standard error of this difference, 0.8; *t* value, 6.

TABLE VIII

NUMBER OF PELVIC AND PECTORAL RAYS IN *GILA*, HYBRIDS, AND *SIPHATELES*

Collection and kind	Number of pelvic rays					No. of counts*	$M \pm \sigma_M$	Hybrid index
	7	8	9	10	11			
Deep Creek collection, September 1, 1934								
Gila orcuttii ...	4	174	22	..	..	200	8.09 ± .02	...
HYBRIDS	..	5	137	58	..	200	9.27 ± .04	73
Siphateles	..	4	50	146	..	200	9.71 ± .04	...
Afton Canyon collection, July 26, 1940								
Gila orcuttii ...	1	332	68	..	..	406	8.17 ± .02	...
HYBRIDS	..	9	96	21	..	126	9.10 ± .04	63
Siphateles	..	1	47	80	2	130	9.64 ± .05	...

Collection and kind	Number of pectoral rays							No. of counts*	$M \pm \sigma_M$	Hybrid index
	13	14	15	16	17	18	19			
Deep Creek collection, September, 1, 1934										
Gila orcuttii ...	1	26	113	58	2	..	..	200	15.17 ± .04	...
HYBRIDS	..	..	16	86	89	8	1	200	16.46 ± .05	139
Siphateles	..	..	33	120	42	5	..	200	16.10 ± .04	...
Afton Canyon collection, July 26, 1940										
Gila orcuttii ...	..	10	61	54	12	3	..	140	15.55 ± .07	...
HYBRIDS	..	1	9	51	59	4	..	124†	16.45† ± .06	220
Siphateles	..	..	43	53	31	3	..	130	15.95 ± .06	...

* Both fins were separately enumerated.

† Not including one count of 0 rays (pectoral fin absent on one side of one fish).

TABLE IX

NUMBER OF ANAL RAYS IN *GILA*, HYBRIDS, AND *SIPHATELES*

Collection and kind	Number of anal rays					No. of specimens	Av.	Hybrid index
	6	7	8	9	10			
West Fork of Mohave River								
Gila orcuttii	..	124	2	..	..	126	7.02	..
HYBRIDS	..	14	38	..	..	52	7.73	75
Siphateles mohavensis	..	1	80	..	..	81	7.99	..
Deep Creek								
Gila orcuttii	3	115	5	..	..	123	7.02	..
HYBRIDS	..	22	91	1	..	114	7.82	84
Siphateles mohavensis	..	3	101	3	..	107	8.00	..
Mohave River, ¼ to 5 miles below Deep Creek								
Gila orcuttii	..	152	2	..	..	154	7.01	..
HYBRIDS	..	3	3	..	..	6	7.50	51
Siphateles mohavensis	..	1	12	1	..	14	8.00	..
Mohave River, Victorville								
Gila orcuttii	1	90	1	..	..	92	7.00	..
HYBRIDS	..	3	15	..	..	18	7.83	86
Siphateles mohavensis	..	2	55	..	..	57	7.96	..
Mohave River, Afton Canyon								
Gila orcuttii	4	87	6	..	..	97	7.02	..
HYBRIDS	1	34	67	4	1	107	7.72	79
Siphateles mohavensis	1	13	176	1	..	191	7.93	..
Soda Lake spring								
Siphateles mohavensis	..	1	75	4	..	80	8.04	..
All localities								
Gila orcuttii	8	568	16	..	..	592	7.01*	..
HYBRIDS	1	76	214	5	1	297	7.76†	78
Siphateles mohavensis	1	21	499	9	..	530	7.97§	..

* Standard error, 0.01.
† Standard error, 0.03.
§ Standard error, 0.01.

This is a most unexpected result, but the increased pectoral-ray count in the hybrid harmonizes with the fact that the pectoral fin in the hybrids is larger than in either parental species, just as the

TABLE X

NUMBER OF DORSAL RAYS IN *GILA*, HYBRIDS, AND *SIPHATELES*

Collection and kind	Number of dorsal rays				No. of specimens	Av.
	7	8	9	10		
West Fork of Mohave River						
Gila orcuttii	3	122	1	..	126	7.98
HYBRIDS	1	43	8	..	52	8.13
Siphateles mohavensis	..	69	11	1	81	8.16
Deep Creek						
Gila orcuttii	3	119	1	..	123	7.98
HYBRIDS	21	89	4	..	114	7.85
Siphateles mohavensis	1	97	9	..	107	8.07
Mohave River, ¼ to 5 miles below Deep Creek						
Gila orcuttii	1	151	2	..	154	8.01
HYBRIDS	..	5	1	..	6	8.17
Siphateles mohavensis	..	11	3	..	14	8.21
Mohave River, Victorville						
Gila orcuttii	4	84	3	..	91	7.99
HYBRIDS	..	18	..	..	18	8.00
Siphateles mohavensis	..	22	..	..	22	8.00
Mohave River, Afton Canyon						
Gila orcuttii	2	65	3	..	70	8.01
HYBRIDS	..	48	15	..	63	8.24
Siphateles mohavensis	..	52	13	..	65	8.20
Soda Lake spring						
Siphateles mohavensis	..	73	7	..	80	8.09
All localities						
Gila orcuttii	13	541	10	..	564	7.99*
HYBRIDS	22	203	28	..	253	8.02†
Siphateles mohavensis	1	324	43	1	369	8.12§

* Standard error, 0.01.
† Standard error, 0.03; hybrid index, 23.
§ Standard error, 0.02.

higher count of scales between the dorsal fin and the lateral line in the hybrids is consistent with the greater depth of the body in the same region. Something in the constitution of the hybrids seems to have been responsible for a better-developed pectoral fin.

The fins of the hybrids show intermediacy in a very interesting structural feature. The appendages of the *Gila* are very tough and

TABLE XI

FREQUENCIES OF BODY-PROPORTION RATIOS IN *GILA*, HYBRIDS, AND *SIPHATELES*

Based on the data used for Table XIII.

100 × standard length / Dorsal to occiput	31	32	33	34	35	36	37	38	39	40	41	No.	Av.	Hybrid index
Males														
Gila orcuttii	..	..	..	1	2	4	1	..	2	..	..	10	36.3	..
HYBRIDS	..	1	1	5	2	1	..	..	..	..	..	10	34.2	62
Siphateles mohavensis	1	2	5	2	..	..	..	..	..	..	..	10	32.9	..
Females														
Gila orcuttii	..	..	..	..	1	..	..	3	5	..	1	10	38.3	..
HYBRIDS	..	..	..	1	1	3	4	..	1	..	..	10	36.3	62.5
Siphateles mohavensis	..	..	..	3	3	4	..	..	..	..	..	10	35.1	..

1000 × standard length / First gill-slit length	67–70	71–74	75–78	79–82	83–86	87–90	91–94	95–98	99–102	103–106	No.	Av.	Hybrid index
Gila orcuttii	11	4	5	..	..	..	..	..	..	..	20	72	..
HYBRIDS	..	..	..	4	9	3	3	1	..	..	20	86	58
Siphateles mohavensis	..	..	..	..	..	2	5	3	9	1	20	97	..

Eye to preopercle / Internarial width	0.75–0.80	0.81–0.86	0.87–0.92	0.93–0.98	0.99–1.04	1.05–1.10	1.11–1.16	1.17–1.22	1.23–1.28	1.29–1.34	No.	Av.	Hybrid index
Gila orcuttii	2	3	7	4	3	1	..	..	..	..	20	0.915	..
HYBRIDS	..	..	..	2	8	6	1	2	1	..	20	1.06	55
Siphateles mohavensis	..	..	..	..	..	4	3	9	1	3	20	1.18	..

Dorsal height / Anal height	1.07–1.09	1.10–1.12	1.13–1.15	1.16–1.18	1.19–1.21	1.22–1.24	1.25–1.27	1.28–1.30	1.31–1.33	1.34–1.36	1.37–1.39	No.	Av.	Hybrid index
Gila orcuttii	2	4	7	6	1	..	..	..	..	..	..	20	1.14	..
HYBRIDS	..	..	1	2	5	8	2	2	..	..	..	20	1.22	50
Siphateles mohavensis	..	..	..	1	..	..	3	6	3	3	2	18	1.30	..

leathery, perhaps in correlation with its life in rapid water, and the fin rays are very strong. The fins of the *Siphateles* have the skin and rays thinner and more fragile. In single collections that were preserved and handled together the caudal fins are intact in nearly all the *Gila* specimens, but are broken in a considerable proportion of the hybrids and in almost all the *Siphateles* specimens. There is a similar difference between the parental species in the thickness and leatheriness of the skin over the body, and in this respect, too, the hybrids are intermediate.

The hybrids are interjacent between the parental species in the relative height of the dorsal and anal fins (Table XI, last item). On the average the *Gila* has the dorsal fin lower but the anal fin higher than they are in the *Siphateles* (Table XIII). The differences, consequently, are emphasized by comparing the ratios between the dorsal height and the anal height. In this ratio the interspecific crosses are exactly intermediate, showing a hybrid index of 50.

The hybrids are also intermediate in the average position of the dorsal fin. This is indicated by the measurements of the predorsal length and of the distance from the dorsal fin to the occiput, when these are expressed in thousandths of the standard length (Table XIII). When the sexes are treated separately and the discordant length of the head is eliminated, the parental species are seen to overlap but little, and the hybrid indices are about 62.

The relatively high dorsal fin and short predorsal space in the *Siphateles* calls for a comparison of the parental species and the hybrids in the ratio between these two values (Table XII). In the smaller fish the hybrids are definitely intermediate in this ratio (the hybrid index is 62). In the adults the dorsal fin of the hybrids decreases less in relative length than it does in either parental species. As a result, it becomes about as long proportionately as in the *Siphateles* (Table XIII). The hybrid index for the quotient, dorsal height to dorsal–occiput interspace, is about 85 in the adult (Table XII).

The other proportionate measurements of the fins (Table XIII, last 6 items) almost equal or even exceed the values for the *Siphateles* (or, in the anal height only, the value for the *Gila*). The constitution of the hybrids apparently causes them to have large fins.

Another ratio emphasizes observed differences between the parental species and the intermediate position of the hybrids. In the

TABLE XII

FREQUENCIES OF PROPORTIONS, DISTANCE FROM ORIGIN OF DORSAL FIN TO OCCIPUT DIVIDED BY DORSAL HEIGHT, IN SPECIMENS OF *GILA*, HYBRIDS, AND *SIPHATELES*

Collection, standard length, and kind	Dorsal fin to occiput / Dorsal height												No.	Av.	Hybrid index
	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1			
West Fork of Mohave River, April 5, 1939; 44 to 85 mm.															
Gila orcuttii	..	..	..	..	..	1	5	3	2	3	2	..	16	1.74	..
HYBRIDS	..	..	1	4	2	3	2	1	..	..	..	..	13	1.43	84
Siphateles mohavensis	..	..	3	6	5	2	2	..	..	..	..	..	18	1.37	..
Deep Creek, September 1, 1934; 51 to 92 mm.															
Gila orcuttii	..	..	..	..	..	1	4	2	5	5	2	1	20	1.79	..
HYBRIDS	..	..	..	..	4	7	2	6	1	..	..	..	20	1.56	85
Siphateles mohavensis	..	..	..	..	8	3	5	2	1	..	..	..	19	1.52	..
Deep Creek, September 1, 1934; 23 to 31 mm.															
Gila orcuttii	..	..	1	7	14	7	1	..	..	..	..	..	30	1.40	..
HYBRIDS	..	3	12	13	2	..	..	..	..	..	..	..	30	1.25	62
Siphateles mohavensis	3	10	12	5	..	..	..	..	..	..	..	..	30	1.16	..

TABLE XIII

PROPORTIONATE MEASUREMENTS OF ADULTS OF *GILA*, HYBRIDS, AND *SIPHATELES*

Expressed in thousandths of the standard length. Each item (range, with mean in parenthesis) derived from ten measurements, except as indicated by subscript numbers. Based on a single large collection made in Deep Creek, Mohave Desert, California, September 1, 1934.

	Males			Females		
	Gila orcuttii	HYBRIDS	*Siphateles mohavensis*	*Gila orcuttii*	HYBRIDS	*Siphateles mohavensis*
Standard length, mm.	51.3–62.1 (57.1)	55.2–72.5 (63.0)	52.1–70.3 (61.6)	55.5–80.8 (67.2)	55.2–87.3 (66.9)	56.0–91.6 (72.5)
Predorsal length	555–592 (570)	531–573 (557)	531–556 (545)	551–615 (585)	567–598 (579)	549–582 (565)
Dorsal to occiput	343–390 (363)	323–359 (342)	315–342 (329)	353–408 (383)	343–386 (363)	336–363 (351)
Prepelvic length	533–562 (550)	536–579 (558)	525–568 (549)	537–565 (551)	554–578 (566)	545–563 (552)
Anal origin to caudal base ..	292–333 (313)	296–317 (307)	292–318 (303)	279–303 (291)	275–308 (292)	277–295 (286)
Caudal peduncle, length	193–225 (213)	185–224 (200)	194–223 (200)	191–212 (203)	184–214 (199)	181–200 (191)
Caudal peduncle, depth	121–142 (132)	130–141 (135)	126–138 (132)	119–131 (124)	123–140 (131)	123–138 (131)
Lateral line to dorsal origin .	156–180 (167)	162–182 (175)	156–179 (165)	143–164 (155)	155–181 (167)	147–168 (161)
Lateral line to pelvic insertion	99–111 (105)	90–119 (101)	86–114 (100)	95–117 (105)	98–108 (103)	82–126 (105)
Body depth	270–297 (286)	266–312 (288)	254–298 (277)	259–300 (278)	276–317 (292)	268–306 (281)
Head length ...	279–302 (288)	293–315 (306)	283–310 (301)	276–305 (290)	302–325 (313)	287–318 (307)
Head depth	204–221 (210)	196–215 (208)	193–216 (204)	198–217 (205)	202–224 (211)	198–214 (205)
Head width	155–169 (162)	149–174 (158)	147–168 (155)	149–176 (163)	156–188 (167)	148–170 (159)
Interorbital width	86–101 (96)	91–100 (96)	85–99 (92)	90–101 (96)	98–111 (103)	90–104 (94)
Internarial width	49–62 (55)	48–59 (53)	45–53 (49)	49–61 (53)	52–61 (58)	45–54 (50)
Suborbital width	31–39 (35)	31–42 (35)	34–40 (37)	35–39 (37)	35–46 (38)	32–42 (37)
Snout length ...	73–87 (79)	75–90 (82)	70–82 (74)	78–88 (82)	79–93 (87)	69–91 (78)
Eye length	61–65 (63)	60–72 (67)	64–73 (68)	54–65 (59)	57–69 (65)	58–69 (65)

TABLE XIII (*Concluded*)

	Males				Females	
	Gila orcuttii	Hybrids	*Siphateles mohavensis*	*Gila orcuttii*	Hybrids	*Siphateles mohavensis*
Eye to preopercle	43–53 (48)	53–61 (57)	51–62 (57)	47–56 (50)	55–65 (61)	53–66 (60)
Opercle length	92–113 (101)	99–107 (104)	96–117 (105)	93–109 (100)	94–114 (106)	101–115 (107)
Upper jaw length	76–87 (81)	77–93 (86)	71–80 (77)	76–98 (85)	85–96 (92)	74–87 (80)
Mandible length	101–112 (107)	100–117 (109)	102–109 (106)	102–116 (108)	107–119 (115)	103–115 (108)
First gill-slit length	68–78 (72)	81–93 (86)	88–101 (97)	68–77 (72)	80–96 (87)	89–105 (97)
Dorsal height	208–244 (219)	218–244 (233)	227–239 (234)	183–209 (200)	207–236 (221)	201–226 $(215)_9$
Dorsal base	106–135 (119)	118–140 (129)	114–128 (122)	105–121 (109)	111–130 (119)	111–127 (121)
Anal height	179–208 (193)	175–201 (191)	167–184 $(178)_9$	164–185 (175)	166–202 (181)	156–177 (166)
Anal base	90–104 (96)	97–114 (103)	91–107 (99)	76–89 (84)	79–102 (93)	85–105 (93)
Caudal, longest ray, lower lobe	228–270 $(243)_9$	256–289 $(272)_9$	257–290 $(279)_4$	208–254 $(235)_9$	245–291 $(270)_8$	....
Pectoral length	193–225 (210)	214–241 (228)	217–238 (224)	172–189 (182)	195–217 (198)	183–195 (188)
Pelvic length	157–188 (167)	169–197 (183)	173–193 (180)	129–153 (144)	157–183 (164)	156–176 (166)

Gila, as compared with the *Siphateles*, the internarial width (the least distance between the anterior nostrils) is relatively large, but the distance from the eye to the preopercle is relatively small (Table XIII). The ratio between the two proportions (Table XI, third item) shows almost no overlap. The values for the hybrids range between the means for the parental species. The hybrid index of 55 is only 10 per cent above one of exact intermediacy.

Other measurements of the hybrids do not conform with the general rule, that the characters of interspecific fish hybrids are intermediate and unlike those of either parental species. Reviewing the figures in Table XIII, we note that the measurements of the hybrids (expressed in thousandths of the standard length) are high and often extreme for the depth of the head, body, and caudal peduncle, for the length of the head and the parts thereof, and, as already noted,

TABLE XIV

PROPORTIONATE MEASUREMENTS OF HEAD PARTS IN ADULTS OF *GILA*, HYBRIDS, AND *SIPHATELES*

Expressed in thousandths of head length. Each item (range, and mean in parenthesis) derived from twenty measurements. Based on data used in Table XIII.

Head part	*Gila orcuttii*	HYBRIDS	*Siphateles mohavensis*	Hybrid index
Head depth	655–772 (719)	650–715 (675)	626–724 (673)	96
Head width	529–602 (562)	479–602 (525)	484–565 (517)	82
Interorbital width	306–352 (331)	301–353 (321)	282–328 (311)	50
Internarial width	168–213 (187)	156–198 (180)	151–172 (163)	29
Suborbital width	109–136 (124)	100–144 (118)	109–133 (121)	200?
Snout length	253–301 (279)	251–298 (272)	232–287 (251)	25
Eye length	187–228 (211)	179–238 (214)	184–241 (219)	37.5
Eye to preopercle	154–186 (171)	173–204 (190)	172–208 (192)	90
Opercle length	318–381 (349)	310–366 (338)	323–380 (349)	...
Upper jaw length	268–299 (284)	247–319 (288)	231–274 (259)	— 16
Mandible length	350–390 (370)	338–390 (363)	338–364 (354)	44
First gill-slit length	233–271 (249)	245–307 (279)	283–339 (319)	43
Average hybrid index (opercle measurement excluded)				62

for the length of the fins. The high values for the measurements of the head parts, as expressed in relation to the standard length, are due chiefly to the large size of the head, for when the measurements of the head parts are given in thousandths of the head length (Table XIV) intermediacy is generally indicated.

Life colors (noted in the field on September 1, 1934, when the large collection was secured in Deep Creek) give the hybrids an obvious intermediate appearance:

General Tone:
Gila: darker
Hybrids: variably intermediate
Siphateles: lighter

Upper Parts:
Gila: blotched with olive-blackish and olive-brassy colors
Hybrids: variably intermediate
Siphateles: relatively uniform, dark olive

Lower Sides:
Gila: silvery, with more gold than in the *Siphateles*, but also with blue reflections; punctulate with olive black
Hybrids: with a mixture of the gold of the *Gila* and the blue of the *Siphateles*
Siphateles: bluish white, with brilliant blue and gold reflections, the blue predominating

Lower Surface:
Gila: blue white anteriorly; creamy posteriorly
Hybrids: (not specified)
Siphateles: bluish white; scarcely cream-colored posteriorly

Sides of Head:
Gila: with brilliant gold reflections, brightest in a bar just behind preopercle
Hybrids: with bright silvery-blue reflections as in the *Siphateles*, and approaching the *Gila* in the amount of gold; a trace of the golden bar behind preopercle in most hybrids (strong in one)
Siphateles: with silvery blue and gold reflections, but with much less gold than in the *Gila;* no golden bar behind preopercle

Region about Base of Paired Fins:
Gila: translucent gold
Hybrids: with some of this color
Siphateles: (not noted, presumably almost colorless)

Dorsal Fin:
Gila: dusky amber, in some fish with a wash of dull reddish or greenish
Hybrids: (not recorded)
Siphateles: olive to rich brown

Lower Fins:
Gila: with a wash of translucent gold, especially on the paired fins; yellower than in the *Siphateles*
Hybrids: varying greatly; in some much as in the *Gila*, in others, about as in *Siphateles;* in still others, rich orange
Siphateles: olive to rich brown basally, paling outward and with a bluish-white border

Preserved specimens (Pl. II) of *Gila* and *Siphateles* usually differ in coloration, and the hybrids tend to be recognizably intermediate. *Gila* specimens are usually rather dark in general tone, ordinarily show a trace of a dark lateral band, and are typically marked with variable dusky spots (regenerated scales). *Siphateles* specimens are commonly lighter, show little trace of a dusky lateral band, and are not marked with darkened scales; the dark margins of the scale pockets, however, tend to be better defined. The hybrids vary from the one extreme to the other, but commonly exhibit intermediate or mixed characters in their coloration.

EXPLANATION OF EXTREME CHARACTERS OF HYBRIDS

As noted above, the *Gila* × *Siphateles* hybrids are extreme, or tend to be so, in a number of characters. They have a longer and deeper head, bigger fins, and a deeper body (particularly above the axis) than one would expect to find, on the generally well-substantiated theory of hybrid intermediacy. The long distance between the origin of the dorsal fin and the lateral line is correlated with a high scale count along this line. Similarly, on the average the pectoral fin in the hybrid is larger and has more rays than it does in either parental species.

Something in the constitution of these hybrids would seem to grant them an especial development of the head region, of the body depth, and of the fins. We cannot refrain from thinking of this development as due to some factor other than the specific genes. It seems more plausible that a basic feature in the metabolism is responsible; that we are dealing with an expression of hybrid vigor. It will be recalled that the verified hybrids among the sunfishes (Centrarchidae) display what seems to be heterosis in their growth, activity, intensity of color, and heaviness of body (Hubbs and Hubbs, 1931–33). Certain of the *Gila* × *Siphateles* hybrids definitely recall some of the sunfish crosses in having an extreme development of the flesh, which has caused the body to be very robust and the nape region to bulge beyond the occiput. High development of the fins has characterized many of the aquarium-produced hybrids in the Poeciliidae.

The attribution of the large heads, deep body, and high fins of these cyprinid hybrids to heterosis finds support in the similarity of these differences to certain character gradients that are commonly

exhibited by fishes. Thus young fish usually differ from old ones in having the head and the fins proportionately larger (but with a slenderer body), and males differ from females in their bigger fins. Southern races typically differ from northern ones, and races living in highly productive waters often contrast with those inhabiting sterile waters by having deeper bodies, larger heads, and bigger fins (Hubbs, 1941b) — in other words, in the same way that the hybrids under treatment differ from the parental species.

EVIDENCE OF BACKCROSSING

There is no indication that the distinctions between *Gila orcuttii* and *Siphateles mohavensis* are being broken down by the mass hybridization between these genera. In a number of characters the hybrids show little overlap with either parental type, and the whole body of evidence on fish hybrids (Hubbs, 1940a: 205–209) leads us to expect that backcrossing, if it occurred, would cause the counts and measurements to overlap. The number of gillrakers is particularly characteristic of the hybrids (p. 360 and Table V), for only 8 per cent of the counts for the hybrids overlap slightly the range of counts for both parental species. The pelvic rays (Table VIII) are typically 8 in *Gila*, 9 in hybrids, and 10 in *Siphateles*. Studies on correlations of counts in species of fish yield no indication that the gillraker and pelvic-ray counts should show any positive correlation within a systematic unit (unless some hybridization is involved). When we examine these counts for the Mohave cyprinids, we find that such a correlation is indicated (Table XV). The Deep Creek specimens of *Gila* with 9 pelvic rays have a higher average number of gillrakers than those with 8 pelvics. The 8 individuals that agree with the hybrids in having 9 pelvic rays and approach them in having 10 gillrakers probably owe this combination of characters to hybridization followed by backcrossing. The hybrids from Afton Canyon show a definitely significant correlation between the number of pelvic rays and gillrakers ($r = 0.34 \pm 0.07$), which indicates that there are included a considerable number of backcrosses with *Gila* and a few with *Siphateles*.

Backcrossing with *Gila orcuttii* is suggested also by the correlation between extremely low (*Gila*-like) counts of gillrakers and a high number (again *Gila*-like) of pharyngeal teeth in the outer row. These again are unrelated characters with no expected correlation. Among

TABLE XV

CORRELATION BETWEEN NUMBER OF PELVIC RAYS AND NUMBER OF GILLRAKERS IN *GILA*, HYBRIDS, AND *SIPHATELES*

Locality		Lowest pool of Deep Creek				Mohave River in Afton Canyon			
No. of pelvic rays*		7	8	9	10	8	9	10	11
No. of gillrakers*	6	..	4	..	..	4	..	..	..
	7	2	22	..	..	15	3	..	..
Gila orcuttii	8	2	94	12	..	58	18	..	..
	9	..	42	2	..	29	13	..	..
	10	..	12	8	..	2	..	..	..
	8	..	..	..	..	2 †	2 †	..	..
	9	..	..	..	..	..	2 †	..	..
	10	..	..	4	..	6	18	2	..
	11	..	..	5	1	5	21	2	..
	12	..	2	24	4	..	14	..	..
HYBRIDS	13	..	2	35	17	..	21	9	..
	14	..	..	47	19	..	14	..	..
	15	..	1	20	11	..	2	2	..
	16	..	..	..	4	..	5	3	..
	17	..	..	2	2	..	7	3	..
	18	..	..	..	..	..	4	..	..
	18	..	..	4	..	..	..	..	..
	19	..	..	..	4	..	..	..	..
	20	..	..	1	3	..	..	2	..
	21	..	..	..	2	..	..	6	..
	22	..	..	2	8	..	11	5	..
Siphateles mohavensis	23	..	5	5	26	..	5	15	..
	24	..	..	5	35	..	15	25	2
	25	..	1	15	30	1	10	15	..
	26	..	..	10	28	..	5	9	..
	27	..	..	4	10	..	1	5	..
	28	..	..	6	2	..	..	..	..

* The pelvic rays were counted on both sides of all specimens. The gillrakers were enumerated for the right side only, except for three specimens of *Siphateles* from Deep Creek and for one *Gila*, twelve hybrids, and one *Siphateles* from Afton Canyon, which were counted on both sides. All possible combinations of counts were tallied.

† The hybrid with 8 gillrakers and the 2 with 9 rakers, on the right side, have 11 rakers on the left side (the entries are doubled because the pelvic rays were counted on both sides).

the hundreds of specimens counted there are only three hybrids with fewer than 10 gillrakers (on one side only), and two of these three

are among the four that have two teeth in the outer row on one or both sides. The data for the five specimens involved follow:

Gillrakers, 8–11; pharyngeal teeth, 1, 5—4, 1
Gillrakers, 8–11; pharyngeal teeth, 2, 4—5, 2
Gillrakers, 9–11; pharyngeal teeth, 1, 5—4, 2
Gillrakers, 12–12; pharyngeal teeth, 1, 5—4, 2
Gillrakers, 13–13; pharyngeal teeth, 1, 5—4, 2

No very extensive backcrossing is indicated, however. As a rule, the hybrids are probably first-generation products, with low fertility.

SUMMARY

The two native fishes of the Mohave River system, *Gila orcuttii* and *Siphateles mohavensis*, probably had a complementary distribution during the Pluvial period of the Quaternary, for the *Gila* is adapted for fluviatile life and the *Siphateles* for a lacustrine existence. Despite an obvious maladjustment, the *Siphateles* has been able to survive, with the *Gila*, in isolated creeks that now constitute the only permanent water in this river system. As a result of this cohabitation the two species have engaged in mass hybridization. Hybrids were estimated to constitute 8 per cent of the minnow population in the entire basin; in the area of mutual occurrence the hybrid ratio rose to 9. Interspecific hybridization in fishes is seldom carried to such a degree. Ordinarily it appears to be selected against, because of its biotic inefficiency. The breakdown of the isolating mechanism is apparently due to the circumstance that in these desert waters the physical rather than the biotic environment is dominant in the struggle for existence.

The intergeneric hybrids of the Mohave, like other hybrids between species of Western minnows [6] and of fishes in general, display their mixed origin by a variety of circumstantial evidence. The hybrid interpretation is in complete harmony with the ecological picture. The hybrids were more resistant than the *Siphateles*, but less so than the *Gila*, to the great flood of 1938. They show intermediacy in numerous characters of the pharyngeal arch and dentition, with a variability unexpected in a species. They exhibit similar intermediacy and variability in the length of the gill slit and in the number and form of the gillrakers. The scale structure is also transi-

[6] See papers by Hubbs and Schultz (1931), Schultz and Schaefer (1936), and Calhoun (1940). We have in preparation several additional papers, with conclusions similar to those here proposed.

tional. With a few noteworthy exceptions the scale and fin-ray counts interpose between those for the parental species. The fins and integument are less leathery than those in the *Gila*, but not so fragile as those in the *Siphateles*. Several critical ratios between different measurements provide further evidence of hybridity. The color is likewise intermediate. In general, the proportionate measurements yield averages that are intercalated between those for the parental species.

In certain respects, however, the hybrids are not intermediate. They are large-headed, deep-bodied, and big-finned. In some measurements they are more extreme in these respects than is either parental species. This is true, for example, of the pectoral fin and of the depth of the body above the lateral line, and these aberrant measurements are reflected, respectively, in an increased number of pectoral rays and of scales in the series between the origin of the dorsal fin and the lateral line. The extreme development of certain parts of the body in the hybrids we cannot attribute to the action of specific genes. The similar differences that appear in certain gradients, particularly those between southern races and northern ones, and between races dwelling in highly productive waters and ones existing in sterile habitats, lead us to believe that the aberrant features of the hybrids have some simple physiological basis. We attribute their extremely big heads, robust bodies, and large fins to heterosis.

There is evidence of a small amount of backcrossing between the hybrids and the parental species, particularly with the *Gila*. Certain unrelated counts, which happen to be low in the *Gila* and high in the *Siphateles*, show a positive correlation that would probably not have arisen in any way other than by backcrossing.

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FIG. 1. *Gila orcuttii*

FIG. 2. Hybrid

FIG. 3. *Siphateles mohavensis*

All scales are of adults

FIG. 4. Lowest pool of Deep Creek, photographed by Laura C. Hubbs on September 1, 1934, when the entire fish population was removed and preserved for the analysis of the natural hybrids

EXPLANATION OF PLATE II

FIGS. 1–3. Adult females from Deep Creek, collected September 1, 1934

FIG. 1. *Gila orcuttii*, 78 mm. in standard length

FIG. 2. Hybrid, 87 mm. long

FIG. 3. *Siphateles mohavensis*, 79 mm. long

FIGS. 4–6. Adults from Afton Canyon (main stream), collected April 6, 1939; 57–58 mm. in standard length

FIG. 4. *Gila orcuttii*, male

FIG. 5. Hybrid, female

FIG. 6. *Siphateles mohavensis*, female

Gila orcuttii, hybrids, and *Siphateles mohavensis* (photographs by Clarence Flaten)

Pharyngeal arches and teeth of *Gila*, hybrids, and *Siphateles* from adults 71–75 mm. long (photographs by Clarence Flaten)

FIGS. 1, 4. *Gila orcuttii*. Teeth, 2, 5 — 4, 2 (one missing on left side represented by alveolus)
FIGS. 2, 5. Hybrid. Teeth, 1, 5 — 5, 1
FIGS. 3, 6. *Siphateles mohavensis*. Teeth, 0, 5 — 5, 0 (one missing on right side represented by alveolus)

Gila orcuttii Hybrid *Siphateles mohavensis*

Gill arches of adult minnows, 91–99 mm. long

THE MOSQUITOES OF THREE SELECTED AREAS IN CHEBOYGAN COUNTY, MICHIGAN *

WILLIAM H. IRWIN

INTRODUCTION

THE data upon which this paper is based are part of the results of a mosquito survey of three areas in Cheboygan County, Michigan. Larvae and adults were collected from early spring until autumn, and the waters in which the larvae grew were analyzed in an endeavor to learn something of their habitat distribution. Owing to the large amount of time consumed in this type of investigation only three areas were selected for intensive study. Mud Lake, Inverness Township, Cheboygan County, Michigan (T. 37 N., R. 2 W. 1st P. M., Secs. 7 and 18), and Bryant's Bog, Cheboygan County, Michigan (T. 37 N., R. 3 W. 1st P. M., Secs. 29 and 30), were chosen first because of their extensive characteristic bog formations, which impound innumerable pools during the spring and early summer of each year. Later, the eastern shore area (area of the Biological Station of the University of Michigan) of Douglas Lake, Cheboygan County, Michigan, was included. Collections were made during the summers from 1935 to 1939 and the springs from 1937 to 1939. Analyses were made of the waters from which larvae were collected during the spring and summer of 1938 and 1939.

The literature on Michigan mosquitoes is scanty. Pettit (1903) reported a few species from Ingham County. Hinman (1935) confirmed Pettit's record of *Uranotaenia sapphirina* Osten Sacken for Michigan by reporting it from Dexter, Michigan. Dyar (1922) recorded one species that had been sent to him by the Army Medical Board at Camp Custer. Matheson (1924) listed several species from Cheboygan County. Jewell and Brown (1929) reported two species

* Contribution from the Biological Station and the Department of Zoölogy, University of Michigan.

from Mud Lake, Cheboygan County. McDaniel (1932) gave a list of species that probably occur in Michigan. Irwin (1941) published a list of forty-three species known to occur in the state.

The writer is indebted to Professor Paul S. Welch, under whose direction the work was done, and to Professor Robert Matheson for permission to work in the mosquito collection at Cornell University and for his verification of certain identifications.

SITUATIONS STUDIED

Except for the lakes mentioned all waters studied were shallow. No pools were found having a depth greater than one meter. Their depths ranged from a few centimeters to about one meter. The bottoms were littered with decomposing leaves, twigs, and humus. Each pool commonly contained débris originating from the surrounding vegetation. Most of the waters were strongly colored and highly turbid. All pools began to dry by evaporation as soon as the ice melted in the spring; this caused concentrations of aquatic life and suspended matter.

Mud Lake

Descriptions of Mud Lake by Goe, Erickson, and Woollett (1925), Jewell and Brown (1929), and Welch (1936a) make unnecessary any general account of it here. For present purposes it is desirable to point out that the lake is surrounded by a large mat, grounded at the periphery and floating at its lakeward edges; that this mat is narrow on one side of the lake and very expansive on the other; that most of of it is of either the Chamaedaphne-Sphagnum or the Carex type; and that this great area of mat impounds extensive quantities of water. For descriptions of subdivisions and the physicochemical features of these waters see Irwin (1942).

Bryant's Bog

Bryant's Bog is near the southwest shore of Douglas Lake, Cheboygan County, Michigan. It has been the subject of many studies during the past thirty years. (For bibliography see Welch, 1936b.) For the purposes of this paper it is necessary only to point out that the major portion of the bog is occupied by an extensive mat enclosing at its center a small remnant of the original open water. The mat is for the most part a mixture of sedges and sphagnum moss.

Pools on the mat are similar to those at Mud Lake, but the temporary ones at the margin between the aspens and the mat ("marginal ditch") are larger and deeper and persist longer during spring. For the physicochemical features of the waters of these pools see Irwin (1942).

Biological Station Area

Since the time available did not allow investigation of the entire Douglas Lake area pools in the vicinity of the University of Michigan Biological Station were chosen for study. The area included about two and one-half miles of shore line at the southeast corner of the lake. Physiographically these situations are distinctly different from the bogs. The pools are confined to the shore area and consist mainly of old beach pools flooded by rains and melting ice and snow. In early spring the pools are not in deep shade, but later on the shade becomes dense over most of the water. The pools covered a larger area, were deeper, and were more exposed to the wind than pools in the bog areas. These conditions caused the water to warm slowly but uniformly.

Grapevine Point

Grapevine Point is a wooded tract of land situated west of the station site and extending to the lake. It has beach pools on its northern and western shores which seldom remain throughout the

TABLE I

Physicochemical Data from Pools of the Grapevine Point Area, 1939

Date	Type of pool	Water depth cm.	Temp. C.	pH	O_2 c.c. per l.	CO_2 p.p.m.	Methyl orange alkalinity p.p.m.	Conductivity reciprocal megohms
5–11	Beach	60	10.0	6.5	1.7	5.0	122.0	225
5–11	Beach	90	13.0	6.5	3.6	3.1	123.0	220
5–11	Beach	75	12.0	7.3	2.7	9.3	120.0	225
5–11	Beach	25	15.0	7.3	4.6	9.7	94.0	250
5–29	Beach	45	15.0	5.6	1.5	7.4	115.0	290
5–29	Beach	75	15.0	5.9	1.5	5.0	130.0	250
5–29	Beach	45	15.0	5.0	2.0	15.0	101.0	200
5–29	Beach	5	20.0	5.9	0.0	28.0	94.0	200
6–17	Beach	15	15.0	6.0	0.1	10.0	135.0	260
6–17	Beach	45	18.0	7.1	1.2	8.0	140.0	300

summer, but in early spring one on the west shore is about 100 meters long and 15 meters wide and has a maximum depth of 1 meter. The other pools are smaller and shallower. Some on the northern end of the peninsula are completely shaded when the trees are in foliage. Others lying parallel to the shore line are shallower still and, consequently, their waters warm more quickly. The bottoms of the pools, which are composed of sand covered with humus, support trees and shrubs. After drying these areas produce herbs similar to those on the surrounding forest floor. For the physicochemical features of these pools see Table I.

Pine Point

About a mile north of the Station, on the east shore of the lake, a group of four pools occurs on an area called Pine Point. A long semipermanent one extends northeastward from near shore until it

TABLE II

Physicochemical Data from Pools of the Pine Point Area, 1939

Date	Type of pool	Water depth cm.	Temp. C.	pH	O_2 c.c. per l.	CO_2 p.p.m.	Methyl orange alkalinity p.p.m.	Conductivity reciprocal megohms
5–12	Sandpit	45	18.0	5.9	5.2	4.2	8.0	95
5–12	Beach	37	15.0	5.4	1.7	26.2	0.0	45
5–12	Beach	45	21.0	6.0	4.0	13.2	11.0	50
5–30	Sandpit	30	18.0	5.6	4.0	7.5	7.5	57
5–30	Beach	30	18.0	5.8	0.3	10.0	0.0	75
5–30	Beach	37	18.5	5.5	4.4	29.0	3.0	135

merges with a swamp one-half mile distant. It has a maximum depth of 0.5 meter and is a semimarsh supporting trees, shrubs, and emergent aquatic plants. Another depression, formed by excavation of sand, contains water during the greater part of spring. The remaining two are beach pools. One lies parallel to the shore line, is nearly one meter deep, and is so overgrown with shrubs that it is shaded even before the leaves are out. The other is not more than 30 cm. deep in early spring and soon dries, although it covers a considerable area. For the physicochemical features of these pools see Table II.

DISCUSSION OF SPECIES

Genus *Aedes* Meigen

Adult mosquitoes of the genus *Aedes* first appeared about the middle of May and by the last of the month were very numerous in wooded regions. They migrated from their breeding pools to all surrounding areas, but remained only where there were an abundance of green vegetation and protection from wind. During the last of May and the first of June many species entered houses, but did not remain, as do some species of Anophelini. Many species occurred in the pools throughout the remainder of spring and summer. Usually there was but one brood a year, and the number of adults decreased rapidly as the season progressed. Lights seemed to attract them very little, though they would cluster around a warm dish as eagerly as around an animal and would try energetically to insert their mouth parts. They were more inclined to attack when the humidity was high and the air warm. Except during unusually mild nights in early spring their attacks stopped about 10:00 P.M. and began about 4:00 A.M., unless they were disturbed. As the morning advanced beyond eight o'clock they retreated to the shaded and more humid areas of trees, where they stayed until late afternoon.

1. *A. aboriginis* Dyar. — Rare for this region; three females taken at Bryant's Bog, May 28, and two at Mud Lake, June 12, 1938; no larvae or males found.

2. *A. aurifer* (Coquillett). — One adult taken at Mud Lake, July 12, 1937; two larvae collected from large mat pools, Mud Lake, May 14, 1938.

Dyar (1922; 1928) states that the larvae live in cranberry bogs particularly, but apparently this is not true for northern Michigan.

Immature specimens of *A. aurifer* taken from waters with principal chemical features as follows: pH, 5.5; dissolved oxygen, 1.5 c.c. per l.; free carbon dioxide, 2.7 p.p.m.; methyl orange alkalinity, 20.0 p.p.m.; conductivity, 42 reciprocal megohms.

3. *A. canadensis* (Theobald). — Adults abundant; taken as early as May 14, 1938, and as late as August 21, 1938. Larvae very abundant and in every natural situation investigated; greatest concentrations in pools on sphagnum mats; earliest seasonal record, April 30, 1938, latest, August 6, 1937; the later seasonal collections made from cold permanent swamp pools.

Immature specimens of *A. canadensis* taken from waters with principal chemical features as follows: pH, 4.0–7.3; dissolved oxygen, 0.0–8.9 c.c. per l.; free carbon dioxide, 1.8–36.5 p.p.m.; methyl orange alkalinity, 0.0–130.0 p.p.m.; conductivity, 37–290 reciprocal megohms.

4. *A. cinereus* Meigen. — Very common; earliest seasonal collections of adults at Mud Lake and in Douglas Lake area, May 29, 1937 and 1939; found during summer; latest seasonal record, August 21, 1938; never taken far from breeding places; usually fly low, about one meter above ground.

First collections of fourth instar larvae taken 10–14 days later than earliest maturing *Aedes* larvae; found in all natural pools except more acid ones of Bryant's Bog mat; most numerous in shallow pools or at margins of deeper ones; earliest seasonal record, May 8, 1939, latest, June 24, 1937.

Immature specimens of *A. cinereus* taken from waters with principal chemical features as follows: pH, 5.0–7.3; dissolved oxygen, 0.0–4.7 c.c. per l.; free carbon dioxide, 1.5–19.5 p.p.m.; methyl orange alkalinity, 0.0–130.0 p.p.m.; conductivity, 42–290 reciprocal megohms.

5. *A. communis* (DeGeer). — Abundant; earliest seasonal record for adults, May 14, 1938, latest, August 3, 1935 and 1936; specimens taken throughout each summer.

Larvae abundant; in all natural pools, particularly in early-drying pools among aspens, beach pools of Douglas Lake area, and shallow swamp pools; absent in pools with abundance of filamentous algae; earliest seasonal record, April 30, 1938, latest, June 29, 1937; scarce during June; all records for June from cool swamp pools.

Immature specimens of *A. communis* taken from waters with principal chemical features as follows: pH, 5.5–7.3; dissolved oxygen, 0.0–5.2 c.c. per l.; free carbon dioxide, 1.5–26.2 p.p.m.; methyl orange alkalinity, 0.0–122.0 p.p.m.; conductivity, 37–225 reciprocal megohms.

6. *A. diantaeus* Howard, Dyar, & Knab. — Two females taken at Mud Lake, June 12, 1937. Larvae fairly common; earliest seasonal record, April 30, 1938, latest, May 28, 1938.

Immature specimens of *A. diantaeus* taken from waters with principal chemical features as follows: pH, 4.0–6.0; dissolved oxygen, 0.6–5.2 c.c. per l.; free carbon dioxide, 1.9–26.9 p.p.m.; methyl

orange alkalinity, 0.0–34.0 p.p.m.; conductivity, 45–155 reciprocal megohms.

7. *A. excrucians* (Walker). — Adults abundant throughout areas studied; invaded houses in evenings and early mornings, but restricted to wooded regions during day; will attack day or night; earliest seasonal record, May 30, 1939; adults still abundant August 21, 1938.

Larvae common in all natural pools examined, but more abundant in partly shaded ones; earliest seasonal record, April 30, 1938, latest, May 29, 1937.

Immature specimens of *A. excrucians* taken from waters with principal chemical features as follows: pH, 4.0–6.5; dissolved oxygen, 0.0–8.9 c.c. per l.; free carbon dioxide, 1.5–19.5 p.p.m.; methyl orange alkalinity, 0.0–123.0 p.p.m.; conductivity, 37–220 reciprocal megohms.

8. *A. fitchii* (Felt & Young). — Most abundant adult mosquitoes in areas studied; are restricted to the wooded regions during day, but migrate to all parts at night; earliest seasonal record, May 29, 1939, latest, August 21, 1938.

Larvae rare within areas investigated; only four specimens taken, three from mat pools of Mud Lake (1, May 8, 1937; 2, May 14, 1938) and one from beach pool, Pine Point, Douglas Lake area, May 12, 1939.

Immature specimens of *A. fitchii* taken from waters with principal chemical features as follows: pH, 5.5-6.1; dissolved oxygen, 1.4–4.0 c.c. per l.; free carbon dioxide, 2.7–13.2 p.p.m.; methyl orange alkalinity, 11.0–20.0 p.p.m.; conductivity, 42–50 reciprocal megohms.

9. *A. flavescens* (Müller). — Adults not found in areas studied; ten larvae taken in beach pools of Biological Station area; earliest seasonal record, May 12, 1939, latest, May 29, 1939.

Immature specimens of *A. flavescens* taken from waters with principal chemical features as follows: pH, 5.6–6.1; dissolved oxygen, 1.5–4.0 c.c. per l.; free carbon dioxide, 5.0–13.2 p.p.m.; methyl orange alkalinity, 11.0-130.0 p.p.m.; conductivity, 50–290 reciprocal megohms.

10. *A. impiger* (Walker). — Rare; adults found in areas investigated during morning and afternoon in wooded sections, but about buildings of Biological Station only in evenings; earliest seasonal record, May 14, 1938, latest, June 12, 1937.

One larva only taken at Mud Lake, from large mat pool exposed to sun; none found at Bryant's Bog; several collected from beach pool at Grapevine Point, Biological Station area; earliest seasonal record, May 11, 1939, latest, May 29, 1937.

Chemical records of water made from beach pool: pH, 7.3; dissolved oxygen, 2.7 c.c. per l.; free carbon dioxide, 9.3 p.p.m.; methyl orange alkalinity, 120.0 p.p.m.; conductivity, 225 reciprocal megohms.

11. *A. implacabilis* (Walker). — The writer found it impossible to separate the females of *A. implacabilis* from those of *A. punctor* (Kirby). Specimens of both species were reared, but no distinguishing characters for the females could be found. To judge from the proportionate number of larvae of the two species, females of *A. implacabilis* must have been common.

Larvae plentiful at Mud Lake and Bryant's Bog; not found in Biological Station area; first to mature in spring; occurred mainly in sunlit pools; few in shaded swamp pools; comprised about 6 per cent of all larvae taken at Mud Lake and approximately 5 per cent of those at Bryant's Bog; earliest seasonal record, April 30, 1938, latest, May 22, 1937.

Immature specimens of *A. implacabilis* taken from waters with principal chemical features as follows: pH, 4.0–6.1; dissolved oxygen, 1.0–4.7 c.c. per l.; free carbon dioxide, 1.9–19.5 p.p.m.; methyl orange alkalinity, 0.0–20.0 p.p.m.; conductivity, 37–155 reciprocal megohms.

12. *A. intrudens* Dyar. — Adults abundant throughout spring and summer; earliest seasonal record, May 12, 1939, latest, August 10, 1935.

There is a wide variation in the characters used for taxonomy. About 50 per cent of adults collected lacked the lower mesepimeral bristles given as a character in the key by Matheson (1929).

Larvae abundant locally; absent at Mud Lake; not taken at Bryant's Bog during spring of 1937, but abundant in that area in pools among aspens and on mat during spring of 1938; abundant in beach pools at Pine Point, Douglas Lake, 1939; earliest record, April 30, 1938, latest, May 12, 1939.

Immature specimens of *A. intrudens* taken from waters with principal chemical features as follows: pH, 4.0–5.9; dissolved oxygen, 0.0–5.2 c.c. per l.; free carbon dioxide, 2.4–26.2 p.p.m.; methyl

orange alkalinity, 0.0–8.0 p.p.m.; conductivity, 45–110 reciprocal megohms.

13. *A. lateralis* (Meigen). — Adults fairly common; earliest seasonal record, May 14, 1938, latest, July 30, 1937; both males and females taken throughout areas studied; adults were small, about the size of those of *A. canadensis* (Theobald), yet, contrary to the statement by Dyar (1922), not able to crawl through ordinary window screens.

First mature larvae found at Bryant's Bog and Mud Lake, May 8, 1937, and in Biological Station area, May 12, 1939; latest seasonal collection, May 29, 1939. Larvae absent from more acid waters of Bryant's Bog mat. Dyar (1922) states they are found in shaded pools, but most of those collected by the writer were from sunlit pools. However, a few specimens were taken in shaded and partly shaded areas.

Immature specimens of *A. lateralis* taken from waters with principal chemical features as follows: pH, 5.4–6.0; dissolved oxygen, 1.7–5.2 c.c. per l.; free carbon dioxide, 4.2–26.3 p.p.m.; methyl orange alkalinity, 0.0–11.0 p.p.m.; conductivity, 45–155 reciprocal megohms.

14. *A. pullatus* (Coquillett). — Rare; two females taken at Bryant's Bog, May 14, 1938, and May 22, 1937; one female at Mud Lake, May 5, 1938.

One larva found in large mat pool at Mud Lake, May 14, 1938; taken from water with principal chemical features as follows: pH, 5.5; dissolved oxygen, 1.4 c.c. per l.; free carbon dioxide, 2.7 p.p.m.; methyl orange alkalinity, 20.0 p.p.m.; conductivity, 42 reciprocal megohms.

15. *A. punctor* (Kirby). — Owing to the writer's inability to distinguish females of *A. punctor* from those of *A. implacabilis* in field collections of adults (see No. 11) the exact magnitude of the populations of each species was uncertain. *A. punctor* females of known identity were secured only by rearing them from previously identified larvae.

Adults apparently abundant; taken in wooded regions day or night; found in and around buildings only during early morning and evening; among first to emerge in spring; earliest seasonal record, May 14, 1938, latest, August 2, 1938.

Larvae abundant in all situations at Bryant's Bog and Mud Lake;

not found in Biological Station area; numerous in cold, shaded swamp pools as well as in exposed pools of mat and aspens; later seasonal records from the cold, shaded pools; earliest seasonal record, April 30, 1938, latest, July 2, 1937.

Immature specimens of *A. punctor* were taken from waters with principal chemical features as follows: pH, 4.2–6.1; dissolved oxygen, 0.0–8.9 c.c. per l.; free carbon dioxide, 1.5–19.5 p.p.m.; methyl orange alkalinity, 0.0–48.0 p.p.m.; conductivity, 35–170 reciprocal megohms.

16. *A. riparius* Dyar & Knab. — Rare; only one male (May 22, 1937) and one female (July 7, 1938) taken; larvae not found.

17. *A. spenceri* (Theobald). — Rare; one female taken at Mud Lake, July 30, 1937; one larva collected in large mat pool, Mud Lake, May 14, 1938; one larva from mat pool, Bryant's Bog, May 22, 1937. Other specimens taken from areas bordering localities noted here.

One larva taken from water with principal chemical features as follows: pH, 5.5; dissolved oxygen, 1.4 c.c. per l.; free carbon dioxide, 2.7 p.p.m.; methyl orange alkalinity, 20.0 p.p.m.; conductivity, 42 reciprocal megohms. Chemical analyses of water containing other larva not available.

18. *A. sticticus* (Meigen). — Adults rare; not taken beyond shelter of woods except in evening; earliest seasonal record, May 14, 1938, latest, August 2, 1938.

One larva found, May 14, 1938, in shaded permanent swamp pool at Mud Lake, the principal chemical features of which were: pH, 5.0; dissolved oxygen, 0.0 c.c. per l.; free carbon dioxide, 1.5 p.p.m.; methyl orange alkalinity, 20.0 p.p.m.; conductivity, 55 reciprocal megohms.

19. *A. stimulans* (Walker). — Adults abundant throughout spring and summer; earliest seasonal record, May 29, 1939, latest, August 21, 1938; specimens taken in wooded areas day or night after the vegetation had been disturbed; found about buildings and in houses only in early morning and evening hours; commonly associated with *A. fitchii* and *A. excrucians*.

Larvae abundant in beach pools at Grapevine Point and Pine Point, Biological Station area; one specimen only taken in large mat pool at Mud Lake; larvae of thirteen other species found in association with larvae of this species; earliest seasonal record, May 11, 1939, latest, May 29, 1937.

Immature specimens of *A. stimulans* taken from waters with principal chemical features as follows: pH, 5.4–7.3; dissolved oxygen, 1.7–4.6 c.c. per l.; free carbon dioxide, 5.0–26.2 p.p.m.; methyl orange alkalinity, 0.0–122.0 p.p.m.; conductivity, 45–250 reciprocal megohms.

20. *A. trichurus* (Dyar). — Common; adults appear early in spring and are present throughout summer; enter houses in early spring; found in wooded regions until early summer, when their numbers decrease noticeably; earliest seasonal record, May 14, 1938, latest, August 10, 1935.

Larvae absent in more acid pools of Bryant's Bog mat; present in most parts of areas studied; earliest seasonal record, April 30, 1938, latest, May 14, 1938.

Immature specimens of *A. trichurus* taken from waters with principal chemical features as follows: pH, 4.2–7.3; dissolved oxygen, 0.0–4.6 c.c. per l.; free carbon dioxide, 1.5–26.2 p.p.m.; methyl orange alkalinity, 0.0–123.0 p.p.m.; conductivity, 37–250 reciprocal megohms.

21. *A. vexans* (Meigen). — Adults not common; fly low, remaining close to ground; taken at various times of day; enter houses only at night; earliest seasonal record, June 26, 1938, latest, August 21, 1938.

Larvae taken in two collections from permanent swamp pools at Mud Lake, June 12, 1937, and from deep shaded pool on mat at Bryant's Bog, May 8, 1937; no chemical analyses of water available.

Unidentified *Aedes* larvae: Two groups of larvae that could not be identified as belonging to any known species were taken in these areas. In all keys these larvae were traced to *A. diantaeus* Howard, Dyar, & Knab, but the descriptions of that species do not fit. Since they have characters so strikingly distinct the following descriptions are given. Reared adults were not secured.

22. *Aedes sp.* — Two specimens collected from pools among aspens at Bryant's Bog, May 22, 1937; water analyses not available.

Description. — Head: wider than long. Antennae: longer than head, slightly enlarged basally, spines fairly large and scattered, 4-haired tuft at middle. Head hairs: upper, 3–4; lower, 3, anteantennal tuft of 2–4 hairs. Lateral abdominal hairs: double on first segment, single on 2–6. Scales of eighth abdominal segment: 11–12, arranged in triangular patch, each scale with long central spine.

Anal segment: longer than wide, not ringed by large plate, dorsal brush of 2 tufts and 2 long hairs, ventral brush of well-developed tufts. Air tube: three times as long as wide, tapering, pecten before middle with 3 detached teeth, pecten tuft of 5–6 hairs located at middle. Anal gills: about twice as long as anal segment, tapering to sharp point.

23. *Aedes sp.* — These specimens were collected from large mat pools at Bryant's Bog and Mud Lake. The earliest seasonal record was April 30, 1938, latest, May 14, 1938. Larvae taken during 1937 and 1939.

All collections of this species were from waters with principal chemical features as follows: pH, 4.0–5.9; dissolved oxygen, 3.4–8.9 c.c. per l.; free carbon dioxide, 2.4–7.5 p.p.m.; methyl orange alkalinity, 0.0–48.0 p.p.m.; conductivity, 40–155 reciprocal megohms.

Description. — Head: rounded, wider than long. Antennae: longer than head, coarsely spined toward tip, 2-haired tuft at middle. Head hairs: upper and lower 1–2 per trichopore, anteantennal tuft of 2–3 hairs. Lateral abdominal hairs: double on segments 1 and 2, single on 3–6. Scales of eighth abdominal segment: 5–7, arranged in one irregular row, sometimes one or two conspicuously out of line; each scale with long central spine. Anal segment: longer than wide, not completely ringed by plate, dorsal brush with one pair of long hairs and one pair of tufts consisting of 3–4 hairs each, ventral brush well developed. Air tube: at least four times as long as wide, tapering, pecten reaching middle and ending in 3 enlarged detached teeth, pecten tuft of 3–5 small hairs located beyond pecten and middle. Anal gills: pointed, twice as long as anal segment. All hairs of larva nearly uniform in diameter from base to apex, decidedly blunt at apex.

Genus *Anopheles* Meigen

The genus *Anopheles* is represented by three species. There are situations within the county that are well adapted for the growth of Anophelini, but they do not lie within the areas under discussion. Most permanent pools harbor a few larvae, however. Specimens were occasionally taken from beach, swamp, and mat pools, but most frequently from the lakeward margin of the mats. Larvae were not found before the middle of May. In these areas no larvae were collected from water totally exposed to the sun.

24. *A. maculipennis* Meigen. — Most common species found in areas studied; earliest seasonal record for adults, June 18, 1939.

Larvae in all natural pools during summer; specimens taken in margins of Mud Lake and Bryant's Bog; also in mat pools, permanent swamp pools, and beach pools in Biological Station area; earliest seasonal record, May 28, 1938, when only young instars were found; larvae present throughout summer.

Immature specimens of *A. maculipennis* taken from waters with principal chemical features as follows: pH, 4.8–5.1; dissolved oxygen, 0.0–0.7 c.c. per l.; free carbon dioxide, 1.5–2.1 p.p.m.; methyl orange alkalinity, 9.0–14.0 p.p.m.; conductivity, 65–70 reciprocal megohms.

25. *A. punctipennis* (Say). — Rare; scattered records of adults obtained throughout summers; earliest seasonal collection of adults, July 7, 1935.

Larvae present scantily in most natural pools in June, July, and August; earliest seasonal collection was of early instars from large mat pools at Mud Lake, May 28, 1938; occasional specimen in lakeward edges of mat in both Mud Lake and Bryant's Bog.

Immature specimens of *A. punctipennis* taken from waters with principal chemical features as follows: pH, 5.1–6.2; dissolved oxygen, 0.0–0.7 c.c. per l.; free carbon dioxide, 1.8–2.1 p.p.m.; methyl orange alkalinity, 0.0–114.0 p.p.m.; conductivity, 47–290 reciprocal megohms.

26. *A. walkeri* Theobald. — Very rare; one female taken at Mud Lake, August 24, 1938; adults common in localities but a few miles distant.

Genus *Culex* Linnaeus

There are four species of the genus *Culex* in the areas studied. Adults appeared about the last of June and were usually present until late autumn.

27. *C. apicalis* Adams. — Abundant; hide in dark recesses of stumps and logs, but most common on green vegetation; not found in or about buildings.

Larvae abundant in all pools after early June; earliest seasonal record, May 28, 1938; present in swamp pools, mat pools, beach pools, and the margins of Mud Lake and Bryant's Bog during June, July, and August.

Immature specimens of *C. apicalis* taken from waters with principal chemical features as follows: pH, 5.0–6.2; dissolved oxygen,

0.0 3.3 c.c. per l.; free carbon dioxide, 1.5–17.5 p.p.m.; methyl orange alkalinity, 0.0 130.0 p.p.m.; conductivity, 47–290 reciprocal megohms.

There is a variation in the number of head hairs of the larvae taken here. Many have two hairs at each trichopore; other specimens were found with hairs arranged in all possible combinations of one to two at each trichopore for both upper and lower head hairs. Repeatedly specimens with such variations were reared. Adults, male and female, coming from these larvae could not be distinguished from those coming from larvae with but one hair to a trichopore.

28. *C. pipiens* Linnaeus. — Rare; taken only from large mat pools at Mud Lake, June 26, 1938. The only adults secured were reared from this collection. Principal chemical features of water were: pH, 6.2; dissolved oxygen, 0.7 c.c. per l.; free carbon dioxide, 1.8 p.p.m.; methyl orange alkalinity, 114.0 p.p.m.; conductivity, 290 reciprocal megohms.

29. *C. restuans* Theobald. — Abundant; adults found in all localities from last of June to early autumn; earliest seasonal record, June 28, 1937.

Larvae abundant in all quiet natural pools and artificial containers; earliest seasonal record, May 28, 1939, when larvae were taken from large mat pool, Mud Lake; specimens collected almost at will after middle of June from any water supply; found in waters at margins in Mud Lake and Bryant's Bog, in both large and small mat pools, and intermittently in the drain basin of the Biological Station septic tank. When oiling was neglected the water in this basin, rich in organic matter, produced great numbers of mosquitoes. Actual count showed 256 larvae in one cup of the water. By the use of traps to capture emerging adults the pool was found to be producing at least 75 adults per square foot (154.8 sq. cm.) of water surface per hour.

Immature specimens of *C. restuans* taken from water with principal chemical features as follows: pH, 5.0–6.6; dissolved oxygen, 0.4–4.3 c.c. per l.; free carbon dioxide, 1.8–30.5 p.p.m.; methyl orange alkalinity, 6.0–11.4 p.p.m.; conductivity, 60–290 reciprocal megohms.

30. *C. salinarius* Coquillett. — Two larvae found in beach pool at Grapevine Point, Biological Station area, July 20, 1936; adults reared from the larvae, no analyses of water available.

Genus *Mansonia* Blanchard

There was only one representative of the genus *Mansonia.*

31. *M. perturbans* (Walker) is a common mosquito. Specimens could be captured any time during the day or night. They were taken throughout each summer for five years. The writer's earliest seasonal record is June 25, 1939; latest, August 18, 1939. No larvae were found.

Genus *Theobaldia* Neveu-Lemaire

Three species of the genus *Theobaldia* were found within the three areas.

32. *T. impatiens* (Walker). — Rare; one female taken at Mud Lake, August 21, 1938; larvae collected once from large mat pool at Mud Lake, June 26, 1938; adults reared from these larvae; associated with *Anopheles maculipennis, Culex apicalis, C. restuans, C. pipiens,* and *Theobaldia inornata.*

The principal chemical features of water were: pH, 6.2; dissolved oxygen, 0.7 c.c. per l.; free carbon dioxide, 1.8 p.p.m.; methyl orange alkalinity, 114.0 p.p.m.; conductivity, 290 reciprocal megohms.

33. *T. inornata* (Williston). — Rare; two larvae taken from large mat pool at Mud Lake, June 26, 1938, and reared. The principal chemical features of water were: pH, 6.2; dissolved oxygen, 0.7 c.c. per l.; free carbon dioxide, 1.8 p.p.m.; methyl orange alkalinity, 114.0 p.p.m.; conductivity, 290 reciprocal megohms.

34. *T. morsitans* (Theobald). — Rather common at Mud Lake; occasional specimens taken in Biological Station area; none found at Bryant's Bog. Adults could not be induced to eat blood meals, but were captured at their resting places, on the bases of trees and stumps near breeding pools.

Larvae common in all deeper pools of Mud Lake mat and swamp; a few taken from shaded portions of beach pool at Pine Point, Douglas Lake; earliest seasonal record (early instar larvae), Mud Lake, May 12, 1939, latest (mature larvae), August 6, 1937.

Immature specimens of *T. morsitans* taken from water with principal chemical features as follows: pH, 4.9-6.0; dissolved oxygen, 0.0–8.9 c.c. per l.; free carbon dioxide, 1.5–36.5 p.p.m.; methyl orange alkalinity, 0.0-36.0 p.p.m.; conductivity, 45–170 reciprocal megohms.

TABLE III

ASSOCIATION OF LARVAE IN THREE SELECTED AREAS IN CHEBOYGAN COUNTY, MICHIGAN

The figures represent the number of times a species was collected in the same pool with other species.

	Aedes aurifer	canadensis	cinereus	communis	diantaeus	excrucians	fitchii	flavescens	impiger	implacabilis	intrudens	lateralis	pullatus	punctor	spenceri	sticticus	stimulans	trichurus	vexans	Anopheles maculipennis	punctipennis	Culex apicalis	pipiens	restuans	salinarius	Theobaldia impatiens	inornata	morsitans
Aedes aurifer	..	1	..	..	..	..	1	..	..	1	..	..	1	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..
canadensis	1	..	21	11	10	21	2	1	1	13	3	8	1	22	2	..	2	6	..	1	..	4	..	..	..	..	..	12
cinereus	..	21	..	8	4	12	1	1	1	5	1	5	1	13	1	..	3	5	..	..	..	2	..	..	..	..	..	10
communis	..	11	8	..	6	9	..	..	2	3	4	8	..	12	..	..	5	7	1	..	..	1	..	..	..	..	..	5
diantaeus	..	10	4	6	..	9	..	..	..	6	4	2	..	7	..	..	1	3	1	..	..	..	..	..	..	..	..	3
excrucians	..	21	12	9	9	..	2	1	..	9	3	6	..	13	1	..	1	5	1	..	..	..	..	..	..	..	..	7
fitchii	1	2	1	..	..	2	..	1	..	2	..	1	1	2	1	..	1	..	..	..	..	..	..	..	..	..	..	..
flavescens	..	1	1	..	..	1	1	..	..	..	..	1	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..
impiger	..	1	1	2	..	..	..	..	..	..	..	1	..	2	..	..	2	1	..	..	..	1	..	..	..	..	..	1
implacabilis	1	13	5	3	6	9	2	..	..	..	2	3	1	13	1	..	..	2	1	..	..	..	..	..	..	..	..	1
intrudens	..	3	1	4	4	3	..	..	..	2	..	2	..	2	..	..	2	3	..	..	..	..	..	..	..	..	..	..
lateralis	..	8	5	8	2	6	1	1	1	3	2	..	..	6	..	..	2	3	..	..	..	..	..	..	..	..	..	1
pullatus	1	1	1	..	..	..	1	..	..	1	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..
punctor	1	22	13	12	7	13	2	..	2	13	2	6	1	..	1	1	1	5	2	..	..	3	..	..	..	..	..	13
spenceri	1	2	1	..	..	1	1	..	..	1	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
sticticus	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	1	..	..	..	..	..	..	..	..	1
stimulans	..	2	3	5	1	1	1	1	2	..	2	2	..	1	..	..	..	4	..	..	..	1	..	..	..	..	..	1
trichurus	..	6	5	7	3	5	..	..	1	2	3	3	..	5	..	..	4	..	..	..	..	..	..	..	..	..	..	2
vexans	..	..	..	1	1	1	..	..	..	1	..	..	..	2	..	1	..	..	..	..	..	..	..	..	..	..	..	1
Anopheles maculipennis	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3	3	3	..	..	..	1	1	..
punctipennis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	6	..	..	..	..	..	..
Culex apicalis	..	4	2	1	..	..	..	..	1	..	..	..	..	3	..	..	1	..	..	6	3	..	1	6	2	1	1	8
pipiens	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	..	1	1	..
restuans	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	6	1	..	..	1	1	2
salinarius	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..
Theobaldia impatiens	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	1	1	..	..	..	..
inornata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	1	1	..	..	..	..
morsitans	..	12	10	5	3	7	..	..	1	..	..	1	..	13	..	1	1	2	1	..	..	8	..	2	..	..	..	..

Genus *Wyeomyia* Theobald

One species of the genus *Wyeomyia* occurs in the region.

35. *W. smithii* (Coquillett). — Common in bog areas; adults emerge throughout spring and summer; larvae occur continuously in pitchers of *Sarracenia purpurea*. Analyses not made of the water in these plants.

ANALYSIS OF SPECIES LIST

Six genera and 35 species of the family Culicidae, subfamily Culicinae, were collected in these areas. The species are distributed among the genera as follows: *Aedes*, 23; *Anopheles*, 3; *Culex*, 4; *Mansonia*, 1; *Theobaldia*, 3; and *Wyeomyia*, 1. Six of the 8 genera and 35 of the 45 species native to the state occur here. Since 75 per cent of the genera and about 80 per cent of the species reported for the state were taken in the three areas it seems that the waters in them, when conditions are favorable, are well adapted to mosquito production.

At times *Uranotaenia sapphirina* Osten Sacken was abundant in adjacent bog situations, and *Culex tarsalis* Coquillett and *Theobaldia incidens* Thomson were taken near by, but not from these areas. Adults of *Mansonia perturbans* occurred commonly throughout the areas, but no larvae were collected. It seems possible that at times these four species might also be produced in the areas studied.

LARVAL ASSOCIATION

Table III shows the association of larvae as found in the three areas studied. The figures represent the number of times a species was collected in the same pool with the other species.

SUMMARY

1. A list of the species of mosquitoes found in the three areas studied is presented. Six genera and thirty-five species of Culicidae, subfamily Culicinae, were collected.

2. Data are given showing the larval association in the three areas.

3. Contrary to previous taxonomic descriptions, many adult specimens of *Aedes intrudens* lack lower mesepimeral bristles, and numerous larvae of *Culex apicalis* show a variation of 1–2 head hairs per trichopore.

4. The variational ranges of the principal chemical features of the waters in which larval specimens of each species (some exceptions) grew are presented.

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THE BREEDING HABITS OF THE RIVER CHUB, *NOCOMIS MICROPOGON* (COPE) *

JACOB REIGHARD †

CONTENTS

PAGE

Introduction 398

Methods of field observation 398

Observations on nesting 401

- Nest building 401
- Location of the nest site 401
- Digging the pit 402
- The stone pile 403
- Behavior of females during nest building 406
- The completed nest 407
- Linear measurements of the nest 408
- Volume of nest materials 408
- Labor involved in building the nest 409
- Time taken to build the nest 410
- Rate of carrying stones 411

Spawning 412

General behavior of the male 413

Nest associates 415

- Accessory males of *Nocomis* 415
- Other species 416
- Hybridization of associates on the *Nocomis* nest 420

Summary 422

Literature cited 423

* Contribution from the Department of Zoölogy, University of Michigan.

† Editor's Note — Professor Reighard died on February 13, 1942, and hence did not have opportunity to see the proof of this paper. The proof was read by Dr. Karl F. Lagler, of the University of Michigan, who did considerable work on the manuscript while Professor Reighard was still alive. Professors Peter Okkelberg and Carl L. Hubbs, both of the University of Michigan, read the manuscript and offered suggestions.

In Professor Reighard's death the Michigan Academy has lost one of its most esteemed members. The idea of organizing a state scientific society was conceived by him early in the nineties, while he was head of the Department of Animal Morphology of the University of Michigan. He served as president of the Academy in 1900.

INTRODUCTION

THESE studies on the breeding habits of the river chub were made in Mill Creek, a tributary of the Huron River, Washtenaw County, Michigan. The part of the stream in which the observations were conducted lies in the NW $\frac{1}{4}$ of Section 18, Scio Township. Here the creek, 2 to 4 rods wide, meanders for half a mile in a northerly direction. In this stretch is a series of three rapids, in which the shallow water runs swiftly and somewhat brokenly over large stones and small boulders. As the channel broadens and deepens downstream toward each rapids the current slackens into a deep pool of relatively still water. Between two successive rapids the water-sorted bottom material grades from large stones upstream to fine gravel and sand downstream, just above the next rapids. From near the break of the lower rapids to a distance of 6 to 8 rods above it the bottom, to some depth, is made up mostly of stones, 2 to 4 inches across, embedded in fine sand and gravel. The creek bed here is fairly smooth, as though paved with the larger stones, and is uniformly covered with slimy brown algae. A few small boulders, a foot or two in diameter, are scattered about this area. The water in this pool is 18 to 24 inches deep, and its surface is nearly smooth. It is on such bottom that the nests are found in Mill Creek. In 1904 and again in 1926 I counted nine nests within a distance of 190 paces; in 1905, eight; in 1915, four. A total of thirty nests were studied in this habitat.

Nest building takes place from mid-April to the end of May, with water temperatures ranging from 15 to 20.5° C. I have watched the construction of nests on various dates from April 20 to May 28 in 1904, 1905, 1915, and 1926.

METHODS OF FIELD OBSERVATION

In making observations I would approach the stream slowly and cautiously with the sun at my back. Visibility was best when the sun was shining and where a screen of heavy foliage on the opposite bank kept the direct light of the sky from reflecting from the water's surface. In the early work a stop was ordinarily made at a distance of 30 to 40 feet to look for nests, with the aid of field glasses. In their initial stages river-chub nests are shallow pits 9 to 12 inches across, and lighter in color than the undisturbed bottom about

them. Later they become conical heaps of stones ranging in size, according to the stage of completion, from low mounds a few inches high and 12 to 15 inches in diameter to tall mounds 10 to 12 inches above the general bottom level and having a diameter of 3 to 4 feet. Such stone piles are locally characteristic only of *Nocomis* and are unmistakable.

Cautious approach was often rewarded by a sight of the fish at work. If they were not present a motionless wait would bring them back to their tasks. These waits often ran from five minutes to half an hour, but a longer wait was usually fruitless. After the fish had been busy for a while I often crept nearer on hands and knees and again stopped for a time, with my head lifted only high enough to enable me to see the nest. So by several stages I advanced stealthily until I was on the edge of the bank, and the fish were little, if at all, disturbed. I avoided all quick movements of hand or head, and did not permit my garments to flutter in the wind. After a time on the bank I often moved toward the nest slowly, with frequent stops, until I stood over it. A water glass (glass-bottomed container) that was sometimes used for closer observation did not disturb the fish for more than a few minutes. It is in this manner that one makes his first approach to a nest, but later approaches, it was found, could be more rapid.

On my first visit to a certain nest it took me half an hour, including stops, to reach it without disturbing the fish. After an absence of an hour and a half I went to the nest without stopping. The fish left, but returned in ten minutes. On my third approach, on the following day, I again walked directly to the nest. Once more the fish left, but it resumed work in four or five minutes. The nesting fish thus accommodates himself very quickly to the observer, who thereafter becomes almost an integral part of the normal landscape of the fish. The fish became adjusted to a group of people much as to an individual; I often brought ten or twelve students to the bank to observe them.

In order to insure accuracy of data it was necessary to gain an acquaintance with the field characters not only of the two sexes of the species primarily under observation, but of all associated fishes as well. To this end collections were made simultaneously in other sections of the same stream and the characters of the various species were learned. To illustrate the kinds and the utility of such in-

dices to species in these studies characters used to distinguish the river chub and associated species are given. The large breeding males of *N. micropogon* are often seven to ten inches in length overall, robust, and with coarse scales as seen in the water. The border of the opercle is dusky, but not black like that in the common shiner (*Notropis cornutus*). No black spot occurs on the dorsal, but there is one in the horned dace (*Semotilus a. atromaculatus*). The front borders of the pelvics and the anal are dead white, being whiter than those in the common shiner. The sides above the lateral line and the lower body surfaces are rosy in the larger males. A band of sharp conical pearl organs runs across the front of the head. In the larger males the area of integument that bears the nuptial tubercles is elevated into a hump, so that in side view the fish seems to have a Roman nose. A dark spot at the caudal base, which is sometimes indistinct, is not round, although it is in the hornyhead, *Nocomis biguttatus*. Young males with tuberculate heads have a well-marked lateral stripe from snout to caudal and are without the rosy color of sides and belly. All these field characters are easily visible as one stands at the side of the nest, and most of them may be seen at a considerable distance with field glasses. They serve to discriminate the river chub, *N. micropogon*, from its somewhat smaller relative, the hornyhead, *N. biguttatus*, with which it might otherwise be confused,[1] especially since the breeding behavior of the two species is much the same.

The females are usually one third to one half the length of the largest males. They are without pearl organs and do not have the rosy belly seen in active males. Along the side of the head and body they have a well-marked dark stripe not found in full-grown males. Their anals and pelvics are bordered in front with white, as they are in the males. The abdomens of those seen about the nest are usually plainly distended with eggs.

It should be noted that the color differences that I have given here are for freshly caught specimens, since death and preservation alter some of these characteristics.

[1] Hubbs (1926) has given descriptions and photographs of the males of the two northern species of *Nocomis*, both of which had previously passed as "*Hybopsis kentuckiensis*," and Hubbs and Lagler (1941) have published photographs of both sexes of *N. biguttatus* and of a male *N. micropogon*.

OBSERVATIONS ON NESTING

Nest Building

I use the word "nest" for that definite, limited area of construction on which or over which the eggs are laid or into which they are deposited. In some species it may be merely a small area of the bottom swept clean by the fish or hollowed out to make a depression; in other species, those of *Nocomis*, for example, it may be a more elaborate construction. The following account of nest building by the river chub is based on the observation of 24 males engaged in the process over a total period of about 42 hours. The individual observation periods ranged from 1 to 7 hours.

Location of the Nest Site

The breeding ground or general area on which the nests of *Nocomis micropogon* are built appear to be largely determined by the character of the bottom. It must afford enough stones of suitable size for nest building. In these areas the water is usually 18 to 24 inches deep (occasionally as deep as 36 inches), and the current is not sufficiently strong to impede seriously the activities of the fish.

Within any one locality favorable for nesting the sites chosen come to lie in groups of two to four. The distances between the nests of such a group range from 1 to 8 rods, with the average approximately 4 rods. Only once have I found two nests side by side and close together. The nearest nests of adjacent groups that are separated by rapids may be 15 rods apart.

I have never seen a male engaged in digging a pit or carrying stones to his pile except when ripe females were near enough to show themselves occasionally. An adjacent quiet portion of the pool or a still water under an overhanging bank, where females may lie, probably plays some part in fixing the nest location within the breeding ground. The suitability of the bottom seems also to be of importance in determining the precise location. The bottom must be loose enough for the pit to be dug to a depth of four to six inches without encountering stones that cannot be moved, and other nests must not be too close.

Only once have I seen a river chub engaged in the selection of a pit site. A large male left a half-completed nest, went upstream a short distance, and tested the bottom here and there by seizing

the projecting stones in his mouth and trying to move them. He presently located a spot, some feet above his former workings, where the bottom had not been disturbed and began to move a few stones out of it. Soon, however, he swam two or three feet farther upstream, again testing the bottom in various places until he reached a small white patch of bottom from which a few stones had already been removed. Here he remained for fifteen minutes, carrying out stones. Then he went back to the immediately previous excavation and removed more stones from it. After twenty minutes he returned to his original nest and carried stones to it, but three or four minutes later was again at the second of the little pits he had dug and put some stones into it. Apparently, then, suitable spots for pit digging are discovered by trial, and the final nest site is selected after several tests.

Digging the Pit

When the male has located a spot from which stones can be readily removed he starts to dig the pit. He seizes any projecting part of a stone that he can get into his mouth, at times jerking it from side to side to loosen it, and then turns partly on one side, lifts the stone, and swims away with it protruding from his mouth. If a stone is too large to be readily dislodged by lifting, the fish may put his opened mouth against it and slide it along the bottom. When a stone has been lifted it may be moved directly out from the pit, to either side, and dropped either at the edge or within some twelve to eighteen inches of it. If the stone is carried to a greater distance, it is transported downstream with the aid of the current and deposited. Nearly all the stones that are removed from the pit are dropped within two somewhat gourd-shaped areas that are in contact with the pit site at their narrower upper ends and grow wider toward their diverging lower ends, which lie two or three feet below. In one nest the upper ends began six inches above the pit. These areas I call "the dumps." On them nearly all the excavated material is deposited.

Only the exposed surfaces of the superficial layer of undisturbed stones on the bottom are dark-colored (on account of the covering of ooze or algae). Their other surfaces and all faces of the underlying stones are clean, and are colored according to the kind of rock. As soon, therefore, as the surface layer of dark stones has been removed

in digging, the pit becomes conspicuous by reason of the contrast of its color with that of the surrounding bottom. The dumps too become well defined and easily recognized by their light color, since the deeper-lying clean stones from the pit are scattered about.

Some of the stones carried to the dump are three to four inches wide, from which size they grade down to small ones one-quarter inch across. They lie intermingled, unsorted, and scattered at random over both dump areas. Several pebbles may be deposited outside them, directly above the pit, and still others below it, between the lower parts of the pit dumps, but they are too scattered and too small to obscure the outlines of the dumps.

The stones that the male removes from the nest may be twice as large as its head and hence may project prominently from its mouth during transportation, but occasionally when it seems to be carrying nothing at all it may spit out sand or gravel. During this act its head is lowered, the mouth is opened, and finally the contents are suddenly discharged. Sand thus spit out is swept downstream, making a small cloud as it goes. There is usually so little of it at the site chosen that it does not form a noticeable deposit below the pit, as it does during the nesting of the horned dace.

The completed pit is a roughly circular, somewhat saucer-shaped excavation, 12 to 15 inches in diameter and 3 to 6 inches deep at its center.

The Stone Pile

For the sake of clearness I continue to describe the nest building as though it were carried through without interruption. But interruptions there are, due to storms, to rapid changes of the water temperature, to the coming of females that do or do not spawn, and to the presence on the nest of other males of *Nocomis* and of individuals of both sexes of several other species of fish that either use it as a spawning place or feed on the eggs. All these happenings, to be described in detail, delay the work and greatly complicate the picture.

Although the movements of females about a male engaged in the construction of a nest may interrupt his work, their advent upon the scene produces certain typical changes in the pace and character of the nest-building activities. Furthermore, while digging the pit the male leaves it from time to time for no apparent cause unless it be to search for hidden females. He goes out of sight

downstream and then, in a minute or two, returns to his work. During his absence and occasionally at other times females enter the pit singly or in groups of five or six. The returning male chases them away; I have never seen them spawn in the pit. The presence of females in and about the pit seemingly speeds the work of digging. The fish seems to work faster under the stimulus of seeing the nest nearing completion.

With the pit more or less completed and with females present the stone-carrying activity of the male is reversed; he begins to bring stones back into it.

Once a male busily engaged in carrying stones from his pit gradually became less active in this work until after 20 minutes he took out only an occasional stone. During this period he had begun to bring stones from distances as great as 8 feet *upstream* and to drop them into the pit or just above it. The activity of carrying out, which at first alternated with that of carrying in, became the less frequent. Finally, in $6\frac{1}{2}$ minutes 24 stones were brought to the pit and none taken out. A little later 18 were brought in within 4 minutes. Another male, after steadily removing stones from his nearly completed pit for 10 minutes, reversed his activities and began to carry nest material in. The first few stones brought in were at once picked up and taken out, but only slightly beyond the excavation. After five minutes of vacillation between carrying them in and carrying them out it steadily brought them in without removing any. Females were seen about both these pits, and they entered one of them. Two other males transported stones both in and out during a 10-minute period, but they were not observed long enough to see whether complete reversal was effected or whether females were present. The coming of females to the pit appears most likely to be the stimulus for the reversal of the stone transportation, for it was repeatedly noted that as the stone pile grew the carrying-in activity was temporarily reversed in the absence of females.

Having once turned completely to filling the pit and building a pile, the male continues the work more or less steadily. Whereas in digging his pit he carries the excavated materials downstream and to either side and deposits them within well-defined dump areas, in accumulating materials for his stone pile he most often goes upstream and brings the stones down to the growing pile, for that is the easier way.

Usually in nest building a male swims up eight feet, or less, and in his workings covers a fan-shaped area above the pit site. Some stones, however, are brought in from downstream, and in time all the larger ones that have been deposited on the dumps are regathered. Wherever he goes, he seizes the projecting parts of stones in his mouth and jerks his head sidewise five or six times in order to dislodge them if they are stuck. If he cannot loosen a stone, he goes to another, and so on until he finds one that he can detach. Then he returns with it protruding from his mouth and drops it into the pit or on the pile. The sizes and kinds of material selected and the methods of transport are as previously described for the methods of excavation, except that little if any sand is brought back. He may return with a valve of a large mussel or with two valves that are still held together by the ligament, or with entire living mussels. A six-inch-long cannon bone of a sheep was added to one nest. Whatever can be tugged loose from the bottom and carried is brought in.

Working in this way the male gradually constructs a pile where he had earlier dug a pit. The stones brought in are often covered with brown ooze on one side, and they usually fall with that side up, so that they may soon conceal the brightly colored stones of the pit bottom. In 55 minutes one male carried in enough stones to cover the pit bottom completely, and at the end of 1 hour and 25 minutes the pit was level-full. In 2 hours and 25 minutes the stones were heaped 2 inches above the plane of the stream bottom. By the following day this male had accumulated enough stones to make a domelike pile 30 inches across and with a maximum height of about 3 inches above the bottom of the creek. Two days later the pile had grown to a diameter of 33 inches and a height estimated to be 6 inches. By this time the male had gone, and the nest was apparently completed; the stones for the heap had been brought together in about $2\frac{1}{2}$ days. The plan of a typical nest and the calculated amount of work involved in its construction are given later in this paper. A nest of a river chub and its construction by the male have been very briefly mentioned by Greeley (1929).

From time to time while the male is building his pile ripe females approach. The male then often stops his building activities, lowers his head very rapidly, and excavates a shallow spawning trough about the width of his body and about one half to two thirds his

length. He does this by tossing or carrying stones from some place on the pile. The long axis of this minor excavation coincides with the current, and it is deeper at its upstream end. I have seen three such trenches made in ninety minutes by the same male. While hollowing out this little trough he stops at short intervals and lies over it with his head slightly elevated and pointed upstream; he then spreads his pectorals and for a fraction of a second rapidly vibrates the part of the body in the region of the vent, thereby rubbing his vent over the stones. This tremor may aid in cleaning the groove or may be an act of self-excitation preliminary to spawning. While the trough is being made or when it is completed a female usually enters and lies in it to spawn, as subsequently described. Spawning completed, the male returns with increased activity to his stone carrying and drops stones into the trough so rapidly that it is soon obliterated. It is filled the more quickly because most of the stones for the purpose are brought only from short distances — from the edge of the nest or from points near it. While filling the trough, especially just after dropping a stone into it, the male may lie in it and, with his vent close to the bottom, may repeat the trembling movement just described. If a female does not enter the trough the male remains near it or lies in it for a time and then slowly resumes the carrying-in of stones and brings them from greater distances. Thus in the course of building his stone pile he digs many spawning troughs and fills them after the eggs have been laid. Even as the male reverses his carrying activity from out to in on completion of the pit, so he changes it many times from in to out and back to in as he digs spawning trenches and fills them with stones. Often several unused depressions are found on the top of a completed and abandoned nest. Although most of them seem to be troughs for which no females were available for spawning, some may be the work of the central stoneroller (*Campostoma anomalum pullum*), which has been observed using the same stone pile.

Behavior of Females during Nest Building

As the males are engaged in nest building the females apparently lie in a shelter downstream from the nest, and are seen only when they approach it from below. This they do either while the male is still carrying stones out of the nearly completed pit or while he is bringing them in to fill it or to build the pile. During the time the

pit is being dug the male may leave it for a short time. Then the half-dozen females that are poised below it may enter it together or one at a time. A female repeatedly picked up a small pebble from the pit, carried it four or five inches beyond the edge, and then returned and dropped it into the middle of the pit. On another occasion several females in company picked up small stones at the pit's edge, carried them out three or four inches, and dropped them. When the male returns he drives away any females that may be in the pit.

After the pit is filled and while the male is away a female may come to it and carry out small stones so that she may dig a little spawning trough. A six-inch female made a trough equal to her own length, three inches wide, and one inch deep. An excavating female may seize many of the small stones brought in by the carrying male and take them out as soon as they are dropped. By thrusts of her head she may repeatedly drive away any other female that approaches. Before being ejected the intruder usually has time to burrow with her head into the pebbles, as though searching for eggs; she then seizes a small pebble and rushes away with it. Four or five females that came to one unguarded nest put their heads down together and burrowed for an instant with vigorous tail lashings, and then rushed away at the approach of the male or an excavating female.

The Completed Nest

A nest on which no fish had worked for three days and which was of typical size and shape (as determined by previous observations) was selected for the following detailed analysis of a completed structure. It was a roughly dome-shaped pile of surface stones lightly covered with algae and fine organic material. The stones lay where they had been dropped or where they had been moved during the excavation of spawning troughs, and gave no evidence that their irregular surfaces had been smoothed by the fish.[2]

[2] Though most completed nests are rough-surfaced, I have seen one with a surface somewhat like that of a rather smooth undulating pavement. The stones composing it seemed to have been often shifted and pressed down, so that they had become fitted together, mosaic-like. Since many stonerollers and common shiners had worked on this nest the smoothing was probably due to the activity of those species rather than to that of the river chub; the nests or spawning troughs of the central stoneroller often have a similar mosaic-like surface.

While I was lifting the stones by the handful off this nest in order to measure them, much black silt and organic matter was washed out from among the stones as well as from them. The top of the pile was a rather level spindle-shaped area that measured five by eight inches and had its long axis at right angles to the stream. From this elevated plateau convex slopes, of nearly uniform curvature, extended to a border that did not deviate from a smooth curve more than two or three inches at any point. There were three depressions, apparently unused spawning troughs, on the slope; two were symmetrically placed a little more than halfway down on the downstream side, and one was at the middle of the upstream curvature.

Linear Measurements of the Nest[3]

The measurements of this nest follow (those with an asterisk beside them are vertical distances downward from the water's surface):

	Inches
1. Stone pile:	
To middle of top	6.5 *
To stream bottom just above upper edge	16.5 *
To bottom just below lower edge	13.0 *
To middle of right side	14.0 *
To middle of left side	13.0 *
Average distance, water surface to nest edge	14 +
Maximum height of stone pile above plane of stream bottom	7.5
Greatest diameter with current	49.0
Greatest diameter across current	37.0
Average diameter	43.0
2. Pit, after being emptied:	
Greatest diameter with current	13.0
Greatest diameter across current	15.0
Average diameter	14.0
Depth at center	4.0

Volume of Nest Materials

The shape of the stone pile made it difficult to calculate its volume from its dimensions. The problem was solved by removing the materials in three- and twelve-quart containers, which were emptied in a single pile on a level spot on the shore. The final appearance and dimensions of this heap were essentially those of the undisturbed nest. After removal of the pile the pit was emptied

[3] Measurements of nests of *Nocomis biguttatus* are given by Hankinson (1932, p. 414).

and the contents were measured. The emptied pit, which was under the center of the pile, had nearly vertical walls. It looked as it did when first completely excavated by the fish.

The measured volume of the nest materials was found to be as follows:

Stone pile, exclusive of material in pit	66.0 quarts
Pit contents	4.5 quarts
Total volume of nest material	70.5 quarts

The largest stone from the pile measured 1.5 by 3.25 inches on the flat surface and was 0.5 to 2.5 inches thick. Others nearly as large were thicker and thus probably bulkier. An apparently average stone was 1.0 inch by 1.25 inches by 1.0 inch.

In order to estimate the total number of stones in the pit and in the pile the three-quart measure was filled with stones taken here and there at random. This random sample contained 100 stones to the quart. Thus it was estimated that a total of 7,050 stones composed the pile and the pit. In addition, there were 35 valves of mussel shells, 2 complete shells, and 5 living mussels; most valves ranged from 0.5 to 2.75 inches long, but one reached a length of 4.25 inches.

Labor Involved in Building the Nest

In transporting a stone to the nest a fish often travels an estimated 12 feet each way and sometimes 20 feet, that is, 24 to 40 feet for the round trip. If we conservatively estimate an average distance of 12 feet for the round trip, we have probably made sufficient allowance for the relatively few trips on which two or more small stones are brought back. At 12 feet per trip the fish would have traveled 84,600 feet, or a little over 16 miles, to accumulate his stone pile. If we assume the nest material to have the weight of broken stone, roughly 100 pounds per cubic foot, their total weight in air would be 235 pounds. Deducting the weight of an equal volume of water (147 pounds — the water displaced would be less than the volume of broken stone), we find the weight in water of the materials brought in to be 88 pounds. If this weight is lifted and carried in 6,000 trips, the average weight per trip is a little over one fifth of an ounce. All the labor of moving this material, together with that of the original excavation, is usually accomplished by a single male.

Time Taken to Build the Nest

It was on June 4, 1926, that I removed the nest described in the preceding section; I left it at 5 : 00 P.M., with the pit empty. When I revisited it at 11 : 00 A.M., June 5, the pit had been refilled, and on one side of it stones were piled a little above and beyond its margin. The water temperature was 15° C. Eighteen hours had elapsed, during about eight of which there was full darkness, and the night had been cold and clear, probably near frost.

I have a fairly complete direct record of the time taken by one male to fill his pit and complete his stone pile:

April 28, 2 : 45 P.M. Male that has been carrying stones out from his pit begins to carry them in. His pit is circular and measures 12 inches across and 3 to 5 inches deep.
3 : 45 P.M. Light-colored pit bottom nearly covered by darker stones brought in by the male.
4 : 00 P.M. All stones of pit bottom covered by dark stones
4 : 10 P.M. Pit level-full.
5 : 00 P.M. Stones heaped 2 inches above pit.
April 29, 10 : 00 A.M. Stone pile 30 inches across and 2 to 3 inches high.
May 1, 2 : 00 P.M. Stone pile 33 inches across and 6 inches high. Stones from 2.5 to 3 inches and down to 0.25 inch across.

The time taken to fill this pit was from 2 : 45 P.M. to 4 : 10 P.M., or 1 hour and 25 minutes. Hence the time that then elapsed until the observation that the pile was completed, at 2 : 00 P.M., May 1, was roughly 69 hours, but three nights were included and possibly no work was done during the early morning period of low temperatures. Probably less than half the 69 hours were spent on the work. The time required to fill the excavation as recorded above was 85 minutes. The pit of the measured nest contained 4.5 quarts of material and the pile 66 quarts. If we assume the 4.5 quarts to have been gathered in 85 minutes, the construction of the pile would have taken, at the same rate, $\frac{66}{4.5} \times 85$, or 1,247 minutes (20.8 hours) of continuous work. The total time for digging the pit and accumulating materials for the pile would then be 20.8 hours plus 1 hour and 25 minutes or, roughly, 22 hours for the measured nest. The two results, less than one half of 69 hours and 22 hours, indicate that between 20 and 30 hours of continuous work was all that was needed to accumulate the stones in the nest.

Rate of Carrying Stones

In the refilling of the pit, as described above, more than 450 stones were brought in, perhaps 600, since the pit was overfilled. By leaving the number at 450 we make allowance for the carrying of more than one stone on some trips. If this required 85 minutes, as it did in the nest in which the filling time was observed, the average time per trip is about 11.3 seconds.

If the 7,050 stones of the measured nest were gathered in 30 hours of continuous work, we may suppose that only about 6,000 trips were required, since more than one stone is sometimes carried at once. Eighteen seconds would then be the average time of a trip. In the filling of the pit that was accomplished in 85 minutes, with an assumed 450 trips, the average duration of a trip was 11.3 seconds, or, on the assumption of 300 trips, 17 seconds.

These rough calculations were verified by actual observation of the rate of carrying. In midafternoon, when the water is warmest and fish are most active, I have counted 18 carrying trips made in four minutes, at an average rate of 13.3 seconds per trip; also in midafternoon, 24 trips in 6.15 minutes, an average rate of 15.6 seconds; again in midafternoon, 9 trips of 1 to 8 feet (2 to 16 feet for the round trip) in three minutes, an average rate of 20 seconds per trip; still again, 9 trips in 105 seconds, at an average rate of 11.6 seconds per trip. These observed rates agree fairly well with the 11.3- to 18-second rate calculated from nest measurements and from the elapsed time of building the measured nest, and they show that the average rate of carrying stones is between 10 and 20 seconds per round trip. Taken together, these data again indicate that between 20 and 30 hours of continuous work is required to fill a pit and to build the stone pile of a nest.

The foregoing results hold for fair-weather conditions. The effect of unfavorable weather on the building rate is shown by the following observations made in 1926:

May 18. Pit found 8 inches square and apparently 3 to 5 inches deep; no male on it.
May 19–24. Weather cold and raining. Nest not observed.
May 24. Pit now larger and oval; estimated size, 8 to 10 inches. Male carrying out.
May 25. Pit level-full and stones piled perhaps an inch above its edges, at 12 : 00 M.

May 26. Overcast and cold; nest not observed.
May 27. Water 14° C. in morning, rising to 16° C. at 1 : 00 P.M. Stone pile apparently about doubled in bulk since the 25th. Not yet of full size.
May 29. Male still at work on the nest.
May 31. Showers.
June 1. No change in the nest; no work in progress on it. Apparently complete.
June 2–3. Cold and windy; nest not visited.
June 4. Nest unchanged.

On account of unfavorable weather between 11 and 14 days were taken to finish this nest and to fill the pit and build the stone pile.

SPAWNING

As already noted (p. 405), the presence of females in or near the nest at any time after the pit has been filled, or nearly filled, results in the male digging a spawning trough. From time to time while thus engaged and just after dropping a stone the male may interrupt his work and lie in the trough for a short time with his head upstream. Thus placed, he spreads his pectorals and rapidly vibrates the body for a fraction of a second so as to rub his vent over the stones.

Thereupon a female may enter and lie at his side, with her long axis oblique to his. He then bends his body, so that his head is turned slightly toward her. His lateral tubercles are thus pressed against her as he crowds her against the side of the trough. While he is pressing against her she may, by swimming forward, escape quickly without spawning. This maneuver may be repeated several times without actual spawning. With or without such preliminary mating activities the female, having entered the trench, may lie belly down on its bottom while the male enters. After entry, the male may turn partly on the side and bend his body slightly with its convex side toward her and the ventrolateral angle pressed against her. She then rises from the bottom, and as she does so the male throws his body to one side and catches her between the body on one side and the upper surface of the spread tuberculate pectoral fin and the lateral pearled surface of the head on the other side. Extrusion of the sex elements takes place at this time. This spawning act is about as rapid as closing and opening the hand. When released the female swims away downstream, no doubt to return again and again. Whether the fertilized eggs fall into the trench and are covered by the stones later brought in or are swept downstream I do not know. The spawning act somewhat resembles that of the horned dace

(*Semotilus atromaculatus*), as described by me (Reighard, 1910), and that of the common shiner (*Notropis cornutus*), as often observed by me and as reported in detail by Raney (1940). The act for the river chub, however, is more deliberate and is preceded by the female lying on the bottom in the spawning trench, whereas in the two other forms the female does not take this preliminary position, but is poised above the bottom when the male first encircles her.

GENERAL BEHAVIOR OF THE MALE

Long observation of the breeding activities of a species of fish under natural conditions reveals much behavior that is no essential part of these activities. The observer comes to think of each species of fish as having, like each race of man, certain general behavior characteristics and a certain type of disposition.

The male river chub is relatively slow in all his movements. He is unhurried in his work of excavation and in the transportation of stones. He moves deliberately, as though he carefully considers each act before executing it. Even the spawning embrace seems slow as compared with that of other cyprinids. In the presence of females, however, he becomes somewhat brisker while digging the spawning trench and while filling it. But at no time does he seem to work with the speed of other breeding minnows of similar habits.

While the male is building his nest a horde of fifty to two hundred fish may intrude at one time, to spawn on it or to seek eggs to eat. He does not try to eject them so consistently as do other minnows. He often moves undisturbed back and forth through the throng. The associated species give way little or much according to the size of the river chub, but only long enough to let him pass. Usually he behaves as though they were not there. The incessant struggles between breeding males, common in some minnows, do not appear to take place between males of *N. micropogon*. Very rarely does an individual thrust with his tuberculate head at another male of his kind or at large males of the common shiner or stoneroller. The large size of his stone pile makes it difficult or impossible for him to keep it free from intruders, and he does not try to do so.[4]

[4] Recording observations made by himself and Hubbs, Hankinson (1932, p. 418) indicated that *Nocomis biguttatus* in general follows the same behavior on its nest, but that the associated spawning males of *Notropis cornutus* busily drive off intruding fish — perhaps in a commensal relation.

I have seen no evidence that there is any gradual process of accommodation by the male to the presence of the regularly associated species or to occasional visitors on his nest; rather they are accepted at once. So familiar also are floating leaves or patches of foam and their shadows that they bring no reaction from the male as they cross the nest. Even a meandering softshell turtle produced only a momentary flurry. All these things are parts of the normal environment. The breeding *N. micropogon* accommodates himself rapidly to the presence of the observer, as already noted (p. 399), though behavior in this respect shows individual differences. When the observer approaches a nest, causing the fishes to leave it, the male may return in four minutes or not for twenty minutes. The variations in the time of return are probably due to a combination of the physiological state of the fish, the immediate force of the sexual urge, and the strength or the nature of the disturbing stimulus that caused him to flee. As I stood beside one nest the male swam toward my rubber boots as though to examine them and then turned and disappeared downstream, but came back almost immediately. Two or three minutes later he repeated this maneuver, but did not return for about a minute and a half. I then cautiously moved a step nearer. He approached me for the third time, then dropped only a little way downstream and at once retraced his course. He paid no further attention to me; he had become fully adjusted to my presence.

When a nest is approached on which there are fishes other than *Nocomis* all may leave. The other species usually return before the river chub; males of the common shiner consistently return sooner. Once when I had approached within eight feet of a nest the *Nocomis* left and did not return for ten minutes, although three large males of the common shiner remained on the nest along with a great number of females of that species and with many males and females of *N. rubellus*. It was twenty minutes before this male began once more to carry stones into the nest, and it was forty minutes before he worked actively and regularly. Meantime the shiners were undisturbed. Again, when I came within ten feet of a nest on which there was a male *Nocomis*, along with six large breeding male stonerollers, the river chub left, whereas the other fish were undisturbed. The males of *Campostoma* and *N. cornutus* are more brightly colored and more active than those of *Nocomis*, and are constantly fighting

and parading, but they accustom themselves more rapidly to an observer. Males of *Nocomis*, more subdued in coloration and less agile, are less aggressive and slower in their accommodation to a watcher. In their movements, color changes, reaction to associated species, and adaptation to the observer they are also found to be relatively slow.

NEST ASSOCIATES

Accessory Males of Nocomis

I have stated that each nest is usually built by a single male. As seen in the field, males differ in size of body, in coloration, in the size of the hump on the head, and sometimes in the details of distribution of the pearl organs on the head, but the last character is visible only to an observer who stands directly over the nest. Without tagging or marking there are no accurate means of distinguishing males of the same size so that they may be recognized from day to day. During several hours of uninterrupted work at a nest one may keep track of a single male and thus be sure that he always has the same fish under observation. When observations cover several days, the progressive accommodation of the male to the observer, together with size, coloration, and indefinable general appearance, affords fair assurance that the same fish is being studied from day to day.

Sometimes one accessory male, rarely two, may work on the nest at the same time with the principal builder, and we need to know how much of the work they do. In such circumstances there is never any difficulty in telling the males apart. In eight of fifteen periods when eleven nests were observed for a total of twenty-six hours only one male was present. In five of the remaining periods one accessory male was present and working part of the time, whereas during two of these periods sometimes one and sometimes two accessories were near by. The supernumerary males were usually smaller than the builder — in one observation they were only half as long — but their tuberculate heads indicated that they were mature. One accessory male was nearly as long as the builder, and another was longer.

In the seven observation periods during which accessory males were present my records show the amount of work done by them to be as follows: (1) in one period the single and smaller accessory did about as much carrying in during seven hours as did the larger

builder; (2) in another period the builder carried stones *to* the nest steadily during two hours, while one, and at times two, accessories carried stones *out* intermittently and so partly neutralized his work; (3) during three periods the single accessory did very little work and in two others he did none. On the whole, we may say that in these seven periods the accessory males present contributed very little to the building of the nest and that during a total of fifteen observation periods the construction work of accessory males was negligible. I have never seen one of them engage in the spawning act. Each nest may thus be regarded as the work of a single male; the *Nocomis* eggs laid there may also be regarded as having been fertilized by a single fish.

Other Species

In addition to harboring mature and immature males and females of *Nocomis* the large pile of loose stones forming the nest studied attracted three other species of minnows.[5] It is an excellent breeding place for many of them, and when the river chub is not on his nest the others use it. Other species that have been observed taking advantage of the stone piles are:

Campostoma anomalum pullum, central stoneroller. — Breeding males are often from six to eight inches long, strongly tuberculate, brightly colored, and very active. As many as six males, usually ranged side by side, may be present at one time, busily digging their spawning troughs in the stone pile, fighting together, and spawning with incoming females.

Notropis cornutus, common shiner. — Breeding males often are six to eight inches long and are also strongly tuberculate, brightly colored, and very active. From one to twenty large males may be poised over the stone pile, fighting continuously, carrying an occasional small pebble at random but without digging spawning trenches, spawning, parading upstream in pairs, and then returning to the nest.

Notropis rubellus, rosyface shiner. — Breeding males, nearly three inches long and bright red on head and back, may often be seen, by an observer standing over the nest, pairing with females and spawning.

[5] Hankinson (1932, p. 415) listed similar spawning associates of *Nocomis biguttatus* in the Saline River, Michigan.

Half of the thirty nests studied for a short time had one or more additional species of fish on it. The other half were unoccupied. Most of them were completed and, apparently, abandoned. In Table I are shown the frequencies with which each species occurred alone or in association with other species on nests under construction.

TABLE I

SPECIES OF FISH SEEN ON *NOCOMIS MICROPOGON* NESTS DURING FIFTEEN OBSERVATION PERIODS

Group number	*Species present*	*Times observed*
1.	*N. micropogon*	1
2.	*C. a. pullum* and *N. cornutus*	1
3.	*N. micropogon* and *N. cornutus*	1
4.	*C. a. pullum* and *N. cornutus*	2
5.	*N. micropogon, C. a. pullum,* and *N. cornutus*	3
6.	*N. micropogon, N. cornutus,* and *N. rubellus*	5
7.	*N. micropogon, C. a. pullum, N. cornutus,* and *N. rubellus*	2
	Total number of nests observed	30
	Number of nests on which fish were present	15
	Number of periods with *N. micropogon* present	14
	Number of periods with *C. a. pullum* present	8
	Number of periods with *N. cornutus* present	12
	Number of periods with *N. rubellus* present	7

In one period of 7 hours no fish other than *N. micropogon* was seen, whereas in the 13 remaining periods *N. micropogon* was present together with one or more of the three associated species (Table I). The river chub was present, alone or with other species, during 14 of 15 periods; *C. a. pullum,* during 8; *N. cornutus,* during 12; and *N. rubellus,* during 7. The last species has never been seen on a nest except in association with *N. cornutus* (five times) or with *N. cornutus* and *C. a. pullum* (twice).

The chub was absent during only one brief observation period on an uncompleted nest. Longer observation would probably have revealed *N. micropogon* on the nest, for when an observer approaches a nest in such a manner as to disturb the fish, either the chub leaves while the associates remain or all leave and the associates return before the nest owner does. In the absence of *N. micropogon* the nest is taken over by associates. It is likely that a chub had recently left one nest found to be occupied by associates, that it was in the neighborhood, and that it would have been seen again had the ob-

servation period been longer. It appears, then, that it is the presence of the working river chub that attracts associates to the nest rather than the nest itself. On one occasion a chub that left its unfinished stone pile to dig two pits near by was followed from its nest to the new locations by all the many associated shiners. The associates go where a builder is at work. There they find not only a suitable spawning place, but probably food in the form of eggs or of materials dislodged by the moving of stones. The behavior of the chub apparently governs their reactions.

When only one to three individuals of *N. cornutus* or only one to three of *C. a. pullum* are on the nest on which *N. micropogon* is at work the picture is simple. The males of *N. cornutus* usually occupy the upstream slope of the stone pile well above the nest surface; their females approach from downstream, singly or a few together, and go to the males one at a time to spawn. A little "knot" of waiting females, much smaller than the males, may gather and keep position in mid-water a little downstream from the males. Among them may be females of the river chub. The stonerollers are usually to be found on the downstream side of the nest, on or near the bottom; their females come to them in similar fashion and may form waiting groups down current, among which may be females of *N. micropogon.* When both the common shiner and the stoneroller are present the picture becomes more complicated. The males of the former, sometimes twenty together, are over the upstream slope of the pile; the latter, as many as six together, are on the downstream slope. Behind these males, and in part over the stoneroller males, is a cloud of many intermingled hovering females of both species and of female river chubs. They form a fan-shaped mass above the lower nest slope, with the point of the fan upstream. The poised females move up and down, so that at a little distance the mass seen edgewise suggests a slowly waving pennant. Immature males of all three species may be included in the mass. So it was in six out of fifteen of my observation periods on associated species.

The situation becomes still more complicated when *N. rubellus* is present along with *N. cornutus*, as it was in five observation periods out of fifteen. The bright red males and the females of this three-inch minnow are then in part intermingled with the swarm of dull-colored females of *N. cornutus* and the few females of *N. micropogon.* Some rosyfaces hover below the others, nearer the nest top, and mostly

extend downstream beyond the other species, a little above the bottom and below the stone pile. Many of the *N. rubellus* individuals thus form a border or fringe to the fan-shaped cloud of mixed females.

In only two of the fifteen periods did I see all three associated species (male stonerollers, several male common shiners, and many rosyface shiners) on the nest together. My field notes do not indicate that the scene was then greatly different from that afforded by the combination of common and rosyface shiners. The maximum number of fish on the nest could only be estimated, not counted. I have seen as many as twenty to thirty adult males of the common shiners and stonerollers and behind them very many females of these two species together, with females of the river chub and immature males of both species, and intermingled with these a great horde of *Notropis rubellus*. The aggregation may have numbered two hundred.

Besides the associated species of minnows on nearly all nests there are other occasional visitors. Once I observed a single hognose sucker (*Hypentelium nigricans*) rooting in the nest in the absence of the male river chub, and twice again I saw this sucker near the nest.[6] It probably feeds on the eggs.

Here I add from my field notes some excerpts recording the occurrence of other species on the *Nocomis* nest.

May 4, 1905: On the upstream edge of the nest are poised some half-dozen large males of *Notropis cornutus*, and below these hang many small males and females of the same species, perhaps twenty-five in all. Along with them are four or five females of *Nocomis* and many bright-red *Notropis rubellus* about three inches long. Through this crowd the smaller of the two river chubs working on the nest comes with his stones and drops them on the upstream, slightly concave, face of the pile. He pays no heed to the common shiners as he passes through the throng, although they give way a little. Sometimes he seems to be unable to reach his destination through the obstructing throng, but backs out and comes to it from a different angle. There seem to be here at one time twenty to thirty individuals of *N. cornutus* and as many of *N. rubellus*. The larger *Nocomis* is given a much wider berth by the other fish than the smaller one, and usually none but the very large *Notropis cornutus* come into contact with him. These he repels with lateral thrusts of the head.

[6] Hankinson (1932, pp. 418–419) reported seeing a male of *Nocomis biguttatus* attack an intruding *Hypentelium*, driving it off.

May 4, 1905: A large *Nocomis* is carrying the stones and occasionally stops to excavate a spawning trough and lie over it. For the most part the nest is occupied by a large number of males of *Notropis cornutus*. One of these is especially large and generally holds the nest against the others, of which there are twenty or thirty. In his absence several somewhat smaller males of equal size take his place. Behind these hover twenty or thirty smaller males and females. There are also two or three stonerollers at work over the nest and a great swarm of *N. rubellus* is present. When nothing else is distinguishable their color can be seen at quite a distance like streaks of red sunlight over the nest. *N. cornutus* is spawning.

May 28, 1905: The stone pile was twelve inches across and three high when I began observing it today. It contains the usual assemblage of *Notropis cornutus* and *N. rubellus*, together with a single large "bald-headed" *Nocomis* and a few females of *Nocomis*. While the *Nocomis* is carrying stones the common shiners crowd over the nest and spawning trench and spawn. Several times after the male *Nocomis* has left the spawning trench about twelve brilliant rainbow darters, *Poecilichthys c. caeruleus*, enter the trench and work head down among the pebbles as though seeking eggs. A soft-shelled turtle, *Amyda s. spinifera*, about six inches long comes from below and, clawing away the nest pebbles with his forefeet, inserts his snout among them and apparently feeds on eggs. At least I can see his jaws move. The shiners and at first the *Nocomis* avoid his head and take position behind him and at his side. Now the *Nocomis* resumes his stone carrying and is soon dropping stones on the nest as usual. Some of them fall on the top of the half-buried head of the turtle. The turtle traverses about one third the diameter of the nest, then suddenly raises his head, apparently sees me, comes to the surface, sticks his head out within four feet of my face, blows out air, then turns and swims downstream.

Hybridization of Associates on the Nocomis Nest

It is obvious that with males and females of three or four species of minnows on the nest top engaged in spawning in large numbers at the same time, there is opportunity for hybridization to take place. The diagram (Fig. 1) shows the usual position of these species on the nest at the time of spawning.

Eggs and milt are extruded during the spawning embrace, which

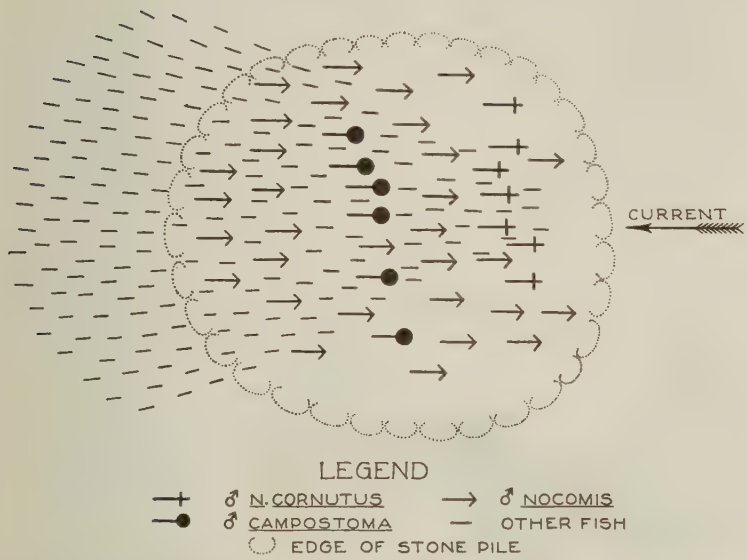

FIG. 1. Diagram showing the usual spawning locus of fishes breeding on the stone-pile nest of the river chub. "Other fish" refers to ripe females and immature males and females of *Nocomis*, *N. cornutus*, and *Campostoma*, and ripe males and females of *N. rubellus*

takes a fraction of a second. The eggs, enveloped in a cloud of milt, are immediately fertilized. The excess milt is swept downstream except as it may be retained for a time in the pockets of stiller water of a spawning trough. If one of these species so placed on the stone pile that its sperm may be carried downstream spawns at a time when the sperm can reach the eggs of another species just as they are extruded, accidental hybridization is possible. The diagram (Fig. 1) shows the usual position on the nest of the breeding males of the three larger species and of males and females of *Notropis rubellus*. Ripe females of all four and males of *N. rubellus* are included in the fan-shaped swarm of small fish below the middle of the nest, from which individual females of the three larger species move up to their males from time to time. There are six possible species crosses and twelve theoretical possibilities if reciprocals are taken into account. *N. cornutus* usually occupies the upstream position, and its sperm

may reach eggs of the other three species. *Nocomis* males may be anywhere on the nest, but are unlikely to be upstream from spawning *N. cornutus*. Their milt may reach eggs of two of the other three species, possibly of all three. *N. rubellus* males, on account of their position, probably will not produce hybrids, but female *rubellus* may cross with males of all the three other species. Females of *N. cornutus*, spawning at the upper side of the nest, presumably may cross only with male *Nocomis*. Of the twelve reciprocal crosses theoretically possible under these circumstances eight are thus possible and four improbable (Table II).

TABLE II

Possible and Improbable Reciprocal Crosses among Fishes Breeding on River Chub Nests

Males	Females			
	Nocomis micropogon	*Notropis cornutus*	*Notropis rubellus*	*Campostoma anomalum pullum*
Nocomis micropogon	...	Yes	Yes	Yes
Notropis cornutus	Yes	...	Yes	Yes
Notropis rubellus	No	No	...	No
Campostoma anomalum pullum ...	Yes	No	Yes	...

SUMMARY

Nests of *Nocomis micropogon* are located in streams in eighteen to twenty-four inches of water, on bottom that affords stones of suitable size for nest building and where the current is not sufficiently strong to impede the activities of the fish.

The nest is constructed by the male, which first digs a pit in the bottom by moving out stones and then fills the pit and builds a pile of stones that, when completed, is rather large.

The principal dimensions and contents of a completed nest pile are: maximum height above plane of stream bottom, 7.5 inches; average diameter, 43.0 inches; volume of materials in pile and underlying pit, 70.5 quarts; number of stones in pit and pile, 7,050.

Work involved in accumulating a stone pile is considerable;

an approximate total of sixteen miles is traveled in about 6,000 trips to and from the nest; weight in water of materials that are transported to build the pile is 88 pounds.

The equivalent of twenty to thirty hours of continuous work by one male is required to build a complete nest; actually this working time may be spread over four days or longer.

Spawning takes place repeatedly on one nest in small troughs excavated on its surface; in the spawning act the sex elements are extruded when the male curves his body over that of the female and holds her for an instant with the side of his head and the pectoral fin, both of which bear nuptial tubercles.

Struggles between breeding males of the river chub rarely occur; neither does the river chub consistently drive other fishes from his nest, as do some other minnows.

Among the nest associates of the river chub are accessory males of the same species that contribute but a negligible amount of work to the construction of the nest.

Breeding associates of the male river chub are mature and immature males and females of the same species, stonerollers, and common and rosyface shiners.

Possibilities of hybridization between breeding associates of the river chub are shown to be either favored or rendered improbable by the positions that they customarily assume about the stone pile.

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ORIGIN OF DIVERSE STRAINS OF AN APHID SPECIES WITHIN A LIMITED AREA *

A. FRANKLIN SHULL

A STRAIN of aphids of the species *Macrosiphum solanifolii* collected in Ann Arbor in the year 1923 was shown to react to light in its developmental processes in such a way that most individuals possessed wings if their late prenatal stages were passed in intermittent light of certain periodicities, but were wingless if those stages were subjected to continuous light. In 1929 that strain experienced a radical change in its behavior, so that thereafter more winged individuals were produced in continuous light than in intermittent, but the difference was not so great. It also produced, after this change, many more intermediate-winged individuals than before (Shull, 1932). This strain was kept nearly ten years longer, during which time its behavior underwent no further material change.

To replace this strain for experimental work another clone was collected in 1931, and found to respond to light precisely as did the 1923 strain at first. It was used incidentally as demonstration material in a genetics class and in January, 1939, unexpectedly produced somewhat more winged offspring in continuous than in intermittent light. The experimental work being done on that strain for some time prior to 1939 had been directed toward other ends, so that the class results were the first indication that the 1931 strain was changing as had its predecessor.

Since a sharp difference in response was essential in the experiments, new strains were collected by Miss Winifred White in the summer of 1939, all of them within a few miles of Ann Arbor. To avoid possible confusion of these aphids with other letter-designated strains that have been so recorded in the literature, these new strains

* Contribution from the Department of Zoölogy, University of Michigan.

may be named M, N, O, P, and Q. They were tested under identical conditions in the fall of that year, and some of them proved to be very different from others. After a period of adjustment to laboratory conditions adult wingless aphids of each strain were reared in intermittent light and in continuous light, and the nature of their offspring noted. The results of these tests are given in the accompanying table.

TABLE I

THE NUMBER OF WINGED AND WINGLESS OFFSPRING PRODUCED BY WINGLESS APHIDS OF FIVE DIFFERENT STRAINS WHEN REARED IN CONTINUOUS AND IN INTERMITTIENT LIGHT (8 HOURS OF LIGHT, 16 HOURS OF DARKNESS)

Strain	Parents in continuous light			Parents in intermittent light		
	Offspring			Offspring		
	Wingless	Winged	Percentage winged	Wingless	Winged	Percentage winged
M	325	0	0	2	318	99.4
N	285	224	44.0	280	49*	14.2
O	471	0	0	172	242	58.5
P	308	0	0	3	340	99.1
Q	514	0	0	199	397	66.6

* In addition, sixteen offspring had intermediate wings.

Two of the five strains (M and P) reacted in the manner desired for experiments. Two produced more winged offspring in intermittent than in continuous light, but the difference was not a sharp one. One actually produced more winged offspring in continuous light than in intermittent, just as did the 1923 strain after its remarkable reorganization in 1929, and as did the 1931 strain in January, 1939. It is possible that only three strains are here represented. M and P could belong to the same clone, though they were collected at places twelve miles apart. O and Q, in view of the number of offspring obtained, could differ as much as they do and still be parts of the same clone, though they were collected five or six miles apart. N is certainly different from the others, but was collected near M. The uniqueness of N is further attested by its production of intermediate-winged individuals.

The existence of diverse strains in one locality raises the ques-

tion how they originated. There are four conceivable methods: (1) each one may have descended from a fertilized egg which lived over the preceding winter, and may owe its difference from other strains to genetic recombination; (2) they may have hibernated in the parthenogenetic phase from unlike strains of the preceding warm season; (3) they may have become different by different mutations from one or more other strains, just as modifications have been observed to occur in the laboratory; or (4) they may have immigrated, already different, from southern latitudes where the parthenogenetic form could overwinter. There are few facts which would definitely indicate a choice among these possibilities with respect to this particular species in the vicinity of Ann Arbor, but certain data bear on the probability of each of them.

GENETIC RECOMBINATION

Genetic recombination in fertilized eggs which existed no farther back than the preceding winter is opposed by the low hatchability of these eggs. In the laboratory, in some experiments with crosses between the red and the green color varieties (Shull, 1925), only a few eggs among the thousands obtained ever hatched. It appears to have been the experience of others who have worked with the fertilized eggs of this species that few of them hatch. Many fertilized eggs were subjected to the rigor of winter, partly indoors and artificial, partly natural, without any increase in the number hatching. It is possible that dietary requirements for hatching are met in nature but not in laboratories. Thus the final autumn generations in nature are supposed to live on rose vines, whereas in laboratory experiments they have mostly been fed the year round on their so-called summer host, the potato. If one or more components of the fertility of mammals are dependent on certain vitamins, it is conceivable that the ability of fertilized aphid eggs to hatch might depend on whether the winged female which laid them fed on the potato or the rose. No one appears to have tested this possibility. If the hatchability is as low in nature as it is in the laboratory, it might seem unlikely that five randomly collected aphids would belong to at least three different strains. A judgment on this point would have to rest on knowledge of the number of fertilized eggs produced, and no data of this sort for southern Michigan are available.

HIBERNATION IN PARTHENOGENETIC PHASE

The overwintering of parthenogenetic aphids would merely push the origin of differences among them back to an earlier date. Such hibernation would, however, permit the strains to be more than one year old (from the fertilized egg), and the age of the strain may have some relation to mutational changes. The two strains in which a change in the response to light (in wing production) was demonstrated had each been reared parthenogenetically for six or seven years before the modification was observed. This fact could be interpreted to mean that an age effect is involved. It also could mean merely that, among the aphids whose response to light mutated, it took a long time for any to be chosen for breeding. Each experiment involved only six or eight females among available hundreds, and random selection of these few breeding individuals could accidentally avoid the mutants for a long time. The chief argument for an age effect is that the age of the two strains was so nearly the same (six or seven years) when the change in response occurred.

Whether this species, *M. solanifolii*, could overwinter in the parthenogenetic phase is questionable. Winter in southern Michigan nearly always involves temperatures as low as −15° to −20° C. one or more times in the season. Some parthenogenetic aphids are known to hibernate in regions having such extremes of temperature at the places where thermometers are kept, but they are mostly root-feeding species, and the temperatures to which they are actually subjected are probably less extreme. There are, however, some indications that species other than root feeders can endure such low temperatures if they are not too prolonged and especially if the cold spells are separated by frequent periods warm enough for some normal activity. On the whole, it seems unlikely that *M. solanifolii* could hibernate out of doors in this region in anything but the fertilized egg stage.

There is the further possibility that the winter is passed, not in outdoor hibernation, but in greenhouses. The parthenogenetic female of this species has a very strong preference for the potato and the rose. Indeed, it is difficult in the laboratory to induce it to stay long on any other plant; starvation seems usually to be preferred to a change of food. In greenhouses, potatoes are seldom available, but some kinds of roses are usually present. Inspection of the green-

houses in or near Ann Arbor has never revealed any of them. These searches have been very careful ones, for aphids were badly wanted when they were made. However, greenhouses in smaller localities where fumigation is less thorough or less frequent might harbor this species. The evidence available seems rather against this form of overwintering, at least in this locality, but is not conclusive.

MUTATION

Origin of differences between strains by means of mutations is obviously suggested by the demonstrated occurrence of such changes in two strains, as reported in this and earlier papers. Presumably mutation in nature is as likely as mutation in confinement, unless some essential condition is not met under natural circumstances. If, for example, mutation cannot happen until the clone is a number of years old, and if all aphids in a northern locality belong to clones which originated not earlier than the preceding spring, it would plainly be impossible for the differences between strains in such an area to arise through mutation.

It should be pointed out that the mutations which have occurred in the laboratory *may* have been environmentally produced, or that environment may at least have contributed to their production. The mutation of 1929 was detected immediately after a series of attempts to eliminate gamic females by means of heat, during which temperatures as high as 31° C. had been applied for long periods. The mutation discovered in January, 1939, occurred in a group of aphids whose ancestors had long been reared at 24° C., though no such change had taken place in a branch of the same clone which was being reared at 14° C. Experiments now in progress are designed to show whether heat may have been responsible for the changes.

The frequency with which mutations can be discovered in these parthenogenetic lines is presumably greatly reduced by the fact that the parthenogenetic eggs are diploid. There is no reduction division in maturation, and no regular recombination of genes. A mutation could hardly occur at a given locus in more than one chromosome of a pair of homologues; hence a recessive mutation would not be detected. Dominant mutations would be discoverable at once, but some sort of chromosomal reorganization would be needed to reveal a recessive mutation.

Mutations in aphids could occur in the mycetome cells, rather

than in the eggs, but presumably only dominant ones would be discovered. Nothing is yet known concerning a possible function of the mycetome in this respect.

IMMIGRATION FROM WARMER REGIONS

It is well known that aphids are carried by wind. It is mostly the winged forms that can be so transported, but in them it is very probable that air currents are more effective than their own active efforts. Winged females appear, in the species under consideration, in any generation after the stem mother, in varying proportions which depend on light, temperature, parentage, and genetic constitution. Winds in the north temperate zone come frequently from the southwest; hence there is every opportunity for aphids to be carried northward, perhaps as rapidly as the season and plant growth advance.

In warm climates these aphids pass the winter in the parthenogenetic phase. It is not necessary to go farther south than Virginia to find *M. solanifolii* more or less active at any time in the winter. Indeed, it has been reported from certain localities that the gamic forms are unknown. A rather moderate migration would suffice to populate the Michigan area with clones which overwintered in the parthenogenetic form farther south. It is conceivable that fertilized eggs might be wholly unnecessary for repopulation each season.

Facts which would help one to form a correct judgment concerning the significance of such migration are mostly lacking. Statistical aid would come from a knowledge of the frequency of physiologically different strains, but the collection and testing of the five clones reported in this paper are the nearest approach to such a census. To know how large an area is covered by a single clone would be helpful, but no information on this point is available. Nothing else is known which would indicate the size of a population unit in these aphids.

One fact seems to stand against immigration from the south, at least as the sole source of the summer population, namely, the occurrence of the pink variety of *M. solanifolii* on the same rose vine in Ann Arbor in three successive years. The vine died at the end of that period, so that the test could be no more extensive. No other rose bush in a number of neighboring blocks in the city bore the pink variety, and many of them not even the more common green variety. It is difficult to believe that random immigration from the

south could each year have planted the pink variety on that particular bush. The alternative supposition, however, is not much more easily accepted. Fertilized eggs of a pink strain, if one assumes with some risk (Shull, 1925) that they would give rise to pink aphids, would presumably have to be deposited on or near that bush each fall. Since the parthenogenetic aphids did not ordinarily remain on this rose all summer, the gamic forms of that or some other pink strain would have had to return to this particular bush. The homing instinct of migrating birds is puzzling enough, without attributing such capacities to still lower orders of life. A further alternative explanation would be to suppose that the same lot of fertilized eggs continued to hatch over several years, but such longevity of fertilized eggs appears not to have been reported.

CONCLUSION

The conclusion appears to be warranted that fertilized eggs have not been abandoned as one of the means of propagation of this species, and that recombination of genes is therefore one of the sources of clonal diversity. Mutation must probably be added to this as a species-wide source of variability. With respect to the population in any limited area immigration from other regions, particularly from the south, should probably be regarded as a more potent factor of variation than it has usually been considered.

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